A FIRST STUDY OF THE INFLUENCE OF THE STARVATION OF THE ASCENDANTS UPON THE CHARACTERISTICS OF THE DESCENDANTS—I

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I. Introductory Remarks

One need not search widely in biological or agricultural literature to encounter discussions of the influence of the conditions to which the ancestors are exposed upon the characteristics of the offspring which they produce. To review here the mass of more or less pertinent literature would lead us too far afield from our present main purpose, which is simply to present the data and state the apparent conclusions from an experimental and statistical study of the influence of starvation and feeding upon the characteristics of garden beans. It is sufficient for the moment to point out that some biologists have attributed a very important rôle to the environment of the mother in determining the characteristics of the offspring. It is perhaps superfluous to say that others of equal authority have expressed diametrically opposite opinions.

The problem is, therefore, a real and an important one. Unfortunately the serious investigator who publishes in this field is sure to be between two large and several

smaller fires. If after cultures of a few generations he finds that the offspring of starved parents do not differ from those which have been well fed, he will be railed at for having wasted his time in demonstrating what was obvious in advance. At the same time he will be criticized by others for not having carried out his experiments "for a sufficient number of generations to allow the accumulation of small effects of the environment" on the ascendants before deciding against the possibility of some influence upon the descendants of ancestral environmental conditions. If he finds that there are measurable differences between series of individuals whose ancestry has been subjected to opposed conditions, the results are sure to be dismissed in many quarters as of little importance because of purely physiological and not hereditary significance.

The very fact of the inevitability of criticism—whatever the results obtained—seems to render it even more highly desirable to appeal to the facts afforded by a large and detailed experimental investigation. Naturally such an experiment can never be so large and so refined as to be beyond all criticism.

The problem is not merely of wide interest from the purely biological viewpoint, but it is of first rate importance from the practical side as well. The biggest pumpkin, the heaviest bull, and the finest ear of corn are the resultant of germ plasm and environment—of nature and nurture, to use Galton's apt words. But in paying fabulous prices for the seed of prize winners little thought is given to the question of the proportionate importance of breeding and feeding in producing this excellence. From the practical standpoint it seems desirable to know whether parents—animals or plants—of as nearly as possible the same hereditary endowment differ at all in their capacity for producing high-grade offspring because of the superior care and feeding which admits them to the show bench. If it be found that the well-fed mother produces finer, or poorer, offspring than the starved one, the practical significance of the result is obvious and the

further biological problems of the nature and permanence of this influence will be open for investigation.

Finally it may be said in passing that the work on these beans was so carried out that data for many other problems besides those discussed here were secured. That of the pure line, that of the relationship between the size of the seed planted and the characteristics of the plant produced, that of the relationship between the size of the plant and the fertility of its pod and the size of the seeds which it produces, that of the relationship between the ovule characters of the pod and its fertility, may be mentioned. These will shortly be made ready for publication; hence if the reader encounters these series of beans in several different places he must not assume duplicate publication. The mass of data in hand is so great that it is either necessary to scatter the material in this way or to withhold it all for several months or years until it can be presented in one volume. The former scheme for several reasons seems the most expedient.

II. Statement of Problems and Description of Materials and Methods

A. *Limitation of the Problem*

The purpose of this paper is to present the results of a series of experiments to determine whether plants whose ancestors have been starved differ from those whose ancestors have been well fed.

It might seem to the reader that the first step in such a problem would be to define starvation and feeding, to list the factors underlying these conditions, and to ascertain the weight of each of these factors in determining the characteristics of a series of plants subjected to them.

This seemed to me in undertaking these particular experiments precisely the course which one should not follow. Physiologists, especially those concerned with plant nutrition in the agricultural stations, have devoted a quarter of a century or more to these very problems.

But concerning the influence of the feeding or starving of the parent upon the characteristics of the offspring, we have little direct experimental knowledge.

It seemed expedient therefore to neglect for the moment the problem of the various edaphic and metereological factors which determine the characteristics of the individual and to ascertain whether the subjecting of parent plants (or parents and earlier ascendants) to differing environmental conditions has any influence upon the characteristics of the offspring. It was therefore only necessary to find fields in which the soil barely sustained a given variety and others which produced a luxuriant growth. The first would represent for the species in question starvation fields.

The judgment of the relative richness of the plots by their actual productiveness is justified by our ignorance of the nature of soil fertility.

The reader who is inclined to criticize this method of approaching the problem as very coarse may be reminded of the following points:

(*a*) The complexity of the problem of soil fertility is such as to preclude a trustworthy evaluation of the particular factors determining the productiveness of any parcel of ground.[1] For this reason I have purposely omitted all but the barest descriptions concerning the experimental plots employed.

(*b*) Artificial soils or water culture media of known chemical composition were carefully considered and ruled out. In the first place, the technical difficulties seemed almost unsurmountable. Again, it seemed desirable to carry on the experiments under conditions as nearly as possible identical with those to be met with in practical agriculture. Chemically prepared nutrient solutions are useful in the physiological laboratory, but they do not occur in practical farming, while soils which are ''sterile''

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[1] Soil experts now agree that chemical analyses of soils furnish no sure criterion of their productiveness.

and those which are "productive"—for what reason we do not know—do.[2]

The solution of our problem is to be sought by means of a series of comparisons which fall into two classes. The first is designed to test the influence of the environment upon the characteristics of the individual; the second is intended to show what influence, if any, the treatment of the ancestors has had upon the offspring.

The first series of comparisons is essential in that it brings out clearly the extent to which the ancestors were modified by the environment to which they were subjected. It affords no evidence whatever as to the factors to which these effects are due. The second set of comparisons is the important one. Our problem, the reader must distinctly understand, is not to determine why some individuals are depauperate and others luxuriant, but whether the rendering of individuals depauperate through the environment to which they are subjected has any influence upon the measurable characteristics of their offspring.

B. Material

The materials upon which this study was based were furnished by five series of garden beans, *Phaseolus vulgaris*. Two of these were the common white Navy. The third was a strain of Burpee's Stringless first grown from commercial seed at the Missouri Botanical Garden in 1905. The other two were from the seed of the White Flageolet and Ne Plus Ultra which Dr. Shull had used in his hybridization experiments.[3]

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[2] Our great ignorance of the problem of soil fertility is attested by the words of Professor Hall in a chairman's address before the Sheffield meeting of the British Association (*Science*, N. S., Vol. 32, p. 364, 1911). He said:

"The fertility of the soil is perhaps a vague title, but by it I intend to signify the greater or less power which a piece of land possesses of producing crops under cultivation, or, again, the causes which make one piece of land yield larger crops when another piece alongside only yields small ones, differences which are so real that a farmer will pay three or even four pounds an acre rent for some land, where he will regard the other as dear at ten shillings an acre."

[3] Shull, G. H., *Science*, N. S., Vol. 25, pp. 792–794, 828–832, 1907; Amer. Nat., Vol. 42, pp. 433–451, 1908.

The two Navy series first came to my attention on the farms of George A. Harris and Elmer Dille at Mount Hermon, near Plantsville, Athens Co., Ohio, in the fall of 1907. From the Harris farm 160 plants were taken, giving rise to 160 "pure lines." These are the Navy *H*, or *NH* series. From the Dille field 550 plants were taken
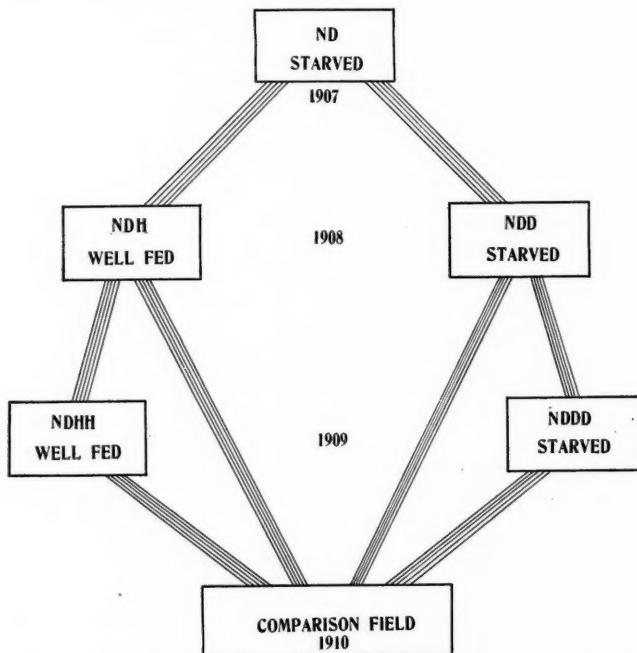

Diagram I. Cultural history of the Navy D series. The history of the Navy H series is the same, and can be expressed by substituting H for D as the first habitat letter in the formulæ.

and yielded 550 "pure lines," designated as the Navy *D* series. These two fields furnished, as explained in detail in a subsequent section, the starvation and feeding tracts of the experiment.

Dr. Shull's seeds saved for individual plants of a crop of 1907 yielded 80 lines of Ne Plus Ultra and 100 of White Flageolet.

The history of these strains during the course of the

experiment is shown by the diagrams. The seriations of number of pods per plant appear in the Data Tables *A*, *B* and *C*.

TABLE *A*

PODS PER PLANT

Series	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total Plants
D	55	229	165	63	24	8	4	1	1	—	—	—	—	—	—	—	550
DD	46	107	141	89	57	36	16	11	3	4	2	—	—	1	—	—	513
DDD	10	61	93	107	67	55	31	24	5	4	—	1	1	—	—	—	459
HD	92	235	333	282	192	135	81	38	11	6	7	1	1	2	—	—	1,416
HDD	49	172	234	208	204	119	84	51	34	22	9	9	3	3	2	1	1,204
USD	53	111	95	30	12	8	3	—	—	—	—	—	—	—	—	—	312
USDD	25	64	42	34	33	19	12	3	1	2	1	—	—	—	—	1	237
FSD	39	100	118	76	43	26	12	13	—	1	—	—	—	—	—	—	428
FSDD	13	52	98	91	64	43	15	4	4	1	—	1	—	1	—	—	387

For convenience of reference I designate the 1907, 1908 and 1909 cultures the ancestral series and the 1910 crops the comparison series. The fitness of these terms will be apparent.

C. *Experimental Methods and Collection of Data*

Experimental methods may conveniently be explained under three heads: Selection and Care of Seed, Cultural Conditions, and Collection of Data.

1. Selection and Care of Seed

The necessary requirements are two. First, it is essential that the material subjected to the various environmental factors shall be identical in its hereditary tendencies. Second, it is essential that in the routine of growing, harvesting and planting no purely physiological (as contrasted with hereditary, germinal or genetic) sources of differentiation shall be introduced.

Consider the first requirement.

We have learned from both biometric and Mendelian researches that it is impossible to know from the simple inspection of an apparently uniform group of individuals whether or not they are really identical as to germinal constitution. It is therefore idle to plant seeds of some individuals under starvation and seeds of other individ-

TABLE B

Number of Pods per Plant

Series	H	HH	HHH	DH	DHH	USS	USH	USHH	FSS	FSH	FSHH
1	—	7	4	9	4	—	—	—	4	—	—
2	—	8	10	10	6	—	1	3	5	1	6
3	1	10	20	16	9	2	2	6	12	4	5
4	4	11	36	21	12	2	5	11	21	4	11
5	3	25	52	20	10	3	5	15	24	9	9
6	4	34	62	20	26	6	8	26	24	6	20
7	6	41	78	29	39	16	15	27	25	14	26
8	7	55	91	26	42	17	20	38	38	12	34
9	10	58	82	36	43	30	17	28	43	22	32
10	12	97	94	43	52	48	40	23	67	32	31
11	9	76	91	35	51	49	17	15	34	24	33
12	12	78	96	39	37	54	22	12	43	22	42
13	12	94	115	34	47	48	28	7	65	22	40
14	9	74	88	34	40	49	25	3	47	24	34
15	7	72	60	28	35	52	23	3	50	25	25
16	7	83	72	35	19	37	26	3	42	23	16
17	9	69	52	35	22	49	18	1	37	19	10
18	8	66	39	30	12	32	13	1	46	27	13
19	5	56	29	24	17	32	20	—	31	19	13
20	1	56	25	21	11	26	13	—	36	17	10
21	4	51	25	16	5	18	12	—	42	19	7
22	3	41	12	9	7	22	6	—	23	12	2
23	5	46	8	13	4	20	3	2	14	23	3
24	3	37	7	11	3	12	5	—	12	8	2
25	2	28	6	5	6	16	4	—	11	11	1
26	2	27	6	8	4	10	2	—	16	12	1
27	2	19	1	9	2	7	3	—	9	12	2
28	4	12	2	7	—	4	5	—	4	13	—
29	1	14	1	10	—	2	1	—	7	7	—
30	2	23	2	5	—	—	1	—	8	2	—
31	1	20	—	2	—	5	—	—	5	6	—
32	—	12	3	3	—	1	—	—	2	2	—
33	—	10	—	5	—	3	—	—	2	4	—
34	1	10	2	3	—	1	—	—	4	3	1
35	—	11	—	3	—	1	—	—	2	4	—
36	1	4	—	2	—	—	—	—	1	1	—
37	1	7	—	4	—	2	—	—	4	3	—
38	—	6	—	3	—	—	—	—	—	1	—
39	—	5	—	1	—	1	1	—	1	—	—
40	1	5	—	1	—	1	—	—	—	1	—
41	—	3	—	—	—	—	—	—	—	2	—
42	—	2	—	1	—	—	—	—	1	—	—
43	—	3	—	—	—	—	—	—	2	1	—
44	—	1	—	—	—	—	—	—	—	1	—
45	—	2	—	1	—	—	—	—	1	—	—
46	1	5	—	—	—	—	—	—	—	—	—
47	—	1	—	—	—	—	—	—	—	—	—
48	—	—	—	1	—	2	—	—	1	—	—
49	—	1	—	1	—	—	—	—	—	1	—
50	—	—	—	1	—	—	—	—	—	—	—
51	—	1	—	—	—	—	—	—	—	—	—
52	—	2	—	—	—	—	—	—	1	—	—
54	—	2	—	—	—	—	—	—	1	—	—
55	—	1	—	—	—	—	—	—	—	—	—
56	—	1	—	—	—	—	—	—	—	—	—
67	—	1	—	—	—	—	—	—	—	—	—
Total plants	160	1,484	1271	670	565	680	361	224	868	475	429

uals of apparently the same uniform variety under feeding conditions.   The only certain method of securing the

TABLE *C*

NUMBER OF PODS PER PLANT

Series	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
HHC	8	8	16	26	35	30	25	31	30	46	25	23	23	21	28	14	18	5	9	8	12	12	11	4	4	2	3
HHHC	8	13	20	34	41	48	38	35	43	37	26	36	25	24	19	17	10	14	15	8	10	8	5	3	4	2	3
HDC	6	10	25	26	29	30	26	28	25	14	12	11	16	23	16	9	10	11	5	5	7	5	4	4	2	3	—
HDDC	11	15	23	35	36	35	32	43	28	34	19	29	32	17	17	10	19	13	15	6	5	4	4	4	1	3	2
DDC	6	16	12	12	20	22	26	14	18	16	8	16	15	15	8	7	4	5	6	1	2	1	1	—	1	1	—
DDDC	6	10	14	23	30	27	27	21	22	23	21	18	16	16	8	6	6	7	3	7	2	1	2	4	2	1	—
DHC	9	21	19	35	41	34	32	33	29	34	25	18	15	13	16	10	8	11	13	7	5	1	7	2	2	1	—
DHHC	7	17	30	38	45	40	52	40	38	34	27	27	19	11	17	19	14	10	9	10	6	1	4	4	4	2	4
USC	3	5	15	22	25	31	48	50	53	69	37	28	31	30	29	15	10	6	6	5	3	2	1	2	1	1	2
USSC	1	—	5	8	10	21	29	31	23	31	43	33	24	28	18	19	19	6	8	8	6	3	3	1	—	3	1
USHC	1	1	7	11	19	28	31	38	18	39	22	22	25	18	8	8	7	7	3	4	1	2	1	—	—	—	
USHHC	2	7	7	13	31	31	31	36	35	41	28	34	27	19	12	6	11	9	5	7	2	1	—	1	—	—	1
USDC	5	10	9	21	42	42	43	43	44	19	22	23	13	15	11	8	5	2	—	1	—	1	—	—	—	—	
USDDC	4	1	7	10	14	22	27	28	36	36	37	28	23	15	13	11	9	7	1	2	1	—	1	—	—	—	
FSC	1	6	9	14	17	29	40	29	26	30	45	38	31	21	31	29	27	13	17	15	18	19	12	14	10	7	6
FSSC	2	6	8	10	13	29	25	28	34	40	30	37	26	35	26	25	25	22	13	17	10	10	8	4	3	2	4
FSHC	—	2	9	18	20	33	30	28	34	21	35	31	19	24	17	14	14	9	11	14	7	7	8	6	5	3	—
FSHHC	—	7	15	20	36	35	31	52	25	38	18	41	39	30	21	19	30	24	21	22	17	11	8	10	12	10	7
FSDC	—	3	6	6	9	14	24	17	21	23	20	26	28	18	9	16	6	7	8	9	11	4	4	1	3	3	2
FSDDC	1	2	8	10	14	23	25	31	32	30	24	40	32	30	32	35	15	15	19	18	16	9	13	15	10	9	5

Series	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	46	47	49	51	52	55	79	Total Plants
HHC	2	5	1	—	—	4	2	1	—	—	—	3	—	—	—	—	—	—	—	—	—	1	—	—	496
HHHC	1	2	—	1	1	—	—	1	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	554
HDC	—	4	1	1	3	—	2	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1	376
HDDC	—	—	2	1	—	2	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	498
DDC	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	255
DDDC	3	—	—	2	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	331
DHC	—	3	1	1	2	—	—	1	2	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	452
DHHC	2	—	1	3	1	—	—	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	538
USC																									530
USSC																									382
USHC																									321
USHHC	—	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	399
USDC	1																								380
USDDC																									333
FSC	2	4	3	6	3	6	1	1	2	1	2	—	—	—	1	—	—	—	—	—	—	—	—	—	586
FSSC	1	1	3	1	—	1	—	—	1	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	502
FSHC	3	3	—	2	2	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	432
FSHHC	10	9	5	5	5	4	3	3	3	—	3	—	1	—	—	—	—	1	—	—	—	—	—	—	651
FSDC	2	—	3	—	—	1	1	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	307
FSDDC	2	3	3	6	2	1	—	—	2	—	1	—	1	2	1	—	1	—	—	—	—	—	—	—	538

desired result is to divide the seeds of individual plants. If this be done and if all the lines[4] be represented

[4] Line or pure line is used merely in the genea'ogical sense.

throughout the experiment by approximately the same number of individuals, we shall not only be sure that like hereditary tendencies went into all branches of the experiment at the beginning, but can feel confident that no material source of error is introduced by a change in the mean hereditary tendencies in either branch of the experiment through the selective elimination (by reason of relative unfitness for the chosen habitats) of certain (differentiated) lines.

These are ideal conditions, quite unattainable among the innumerable difficulties of practical experimentation. Omitting all particulars, I believe we may with reasonable security consider the seeds which went into the original starvation and into the original feeding series random samples from the same individual plants. These lines were maintained with moderate success throughout the experiment.

The following details concerning the methods of manipulating the material may not be irrelevant.

Every seed was, so far as could be determined by inspection, perfectly formed and developed.[5] No seeds in which the coats were sensibly wrinkled were included, since this might indicate either a premature drying of the seed in the pod, or a subsequent wetting.[6]

In harvesting, the plants were left in the field as long as possible to allow the pods to ripen. They were then gathered, and wrapped intact in newspaper to permit any possible translocation of remaining plastic materials from the stems or the pod walls to the seeds.[7]

[5] Every seed was examined at least once. Unfortunately this can not preclude the possibility of a seed containing a weevil which had not emerged up to the time of planting. A large proportion of the seeds planted in these experiments was also weighed individually for use in pure line and other investigations. Of course the seeds giving rise to the plants with which the experiments originated—the NH, ND, US, FS and BG individuals—form a necessary exception to this rule.

[6] I have carried out no experiments to determine what the real causes are of this wrinkling.

[7] This precaution applies to only two of the original series, to NH and ND, but not to FS, US and BG.

2. Cultural Conditions

Having prefaced that the purpose of this study is not to determine what chemical and physical factors produce in the individual the effects which we designate as starvation, we are free to choose for the ancestral series any plots which present reasonably extreme conditions of starvation and feeding.

The two fields in southeastern Ohio seemed perfectly adapted to the purposes of the experiment. Their crops of the common Navy beans presented the most diverse appearance. The *H* field—that grown by Mr. Geo. A. Harris bore a moderately heavy crop. The *D* field—grown by Mr. Elmer Dille—seemed to have almost if not quite as good a stand, but the plants were exceedingly small.

The differences were apparently not due to variety, for both were, in so far as could be seen, identical. They were obviously not referable to cultivation, for both had been equally well tended. The differences seemed entirely attributable to the exceedingly poor soil of the *D* field.

Minute description of these two fields is quite unnecessary. They were about a mile apart, and hence under the same general conditions of climate. Neither was level. Field *H* was much longer than wide and sloped from the ends towards the middle, where the ground was apt to be a little too damp. Plot *D* was situated on an exposed ridge where practically all the surface soil had washed away.

The plants originally growing upon these fields formed the starting point for the starvation-feeding comparison. This was in the fall of 1907. In 1908 transfers were made, in order that we might be sure that genotypically, as the pure linist would have it, the plants cultivated on both fields were the same. Other varieties were also added in 1908. These points are made quite clear by the diagrams.

The comparison furnishing the test of the influence of

the *D* and *H* conditions upon the offspring should not be made on either of these fields.[8]

Three fields[9] under control of the Station for Experimental Evolution at Cold Spring Harbor were chosen for the comparison. All the Navy series were tested
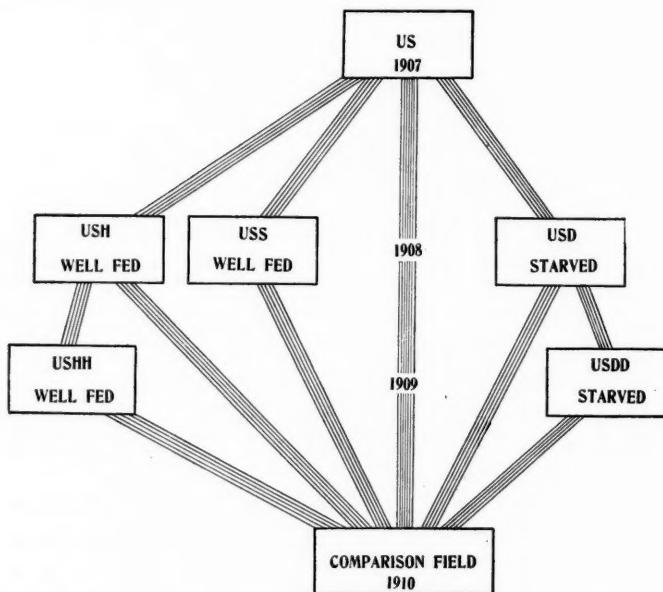
Diagram 2. Cultural history of the Ne Plus Ultra (U) series. The White Flageolet (F) series was subjected to an identical treatment.

on one field and all the Ne Plus Ultra and White Flageolet on another. The third field was devoted to the

[8] A number of breeders hold that among plants there is a gradual adaptation to the substratum; that when plants are transferred from one locus to another there is a "new place effect." If, now, the series grown on the starvation field for two years should from some such process of adaptation be better able to thrive under these conditions than a series newly transferred there from a rich soil, or *vice versa*, the comparison would be an obviously unfair one.

The facts bearing upon this point derivable from our material will probably be discussed later.

[9] Three were selected because accidents of season and culture do occur and it is as unwise to plant all one's experimental seed on a single field as to carry all one's pedigreed eggs in one basket.

fourth variety, *BG,* which must be reserved for a later paper.

The following method was adopted for counteracting the possible hetereogeneity[10] of the fields upon which the plants were grown.

The different strains must be subjected to as nearly as possible a random sample of the conditions afforded by any plot. This end is secured by labeling each seed individually and then scattering those of a particular series quite at random over the field. If, then, certain spots are somewhat more fertile or slightly moister than others, all lines will have equal chances of being represented there. If this were not done an undetected differentiation in the substratum might induce quite deceptive differences in the crops.

In these experiments I did not, unfortunately, work to quite this degree of refinement. For technical reasons, it was desirable to have each of the varieties planted in separate rows. Each seed was placed in an individually labeled envelope and the envelopes of a series thoroughly shuffled. The series were then planted in rows, which were scattered as nearly as possible at random across the field. By this means an almost *but probably not quite* random distribution was secured.

3. Collection of Data

The recording of the data from the mature plants was an onerous but relatively simple process.

As noted above, the plants were wrapped individually at harvest time when as nearly dry as they could be

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[10] Conditions were not worse than those under which much of the experimental evolution work has been done. At the same time I must frankly confess that to the biometrician the comparison fields left much to be desired. Neither of the three was at all level and consequently not of uniform soil texture, fertility or moisture. They were, however, the best available. In stating that conditions are in defect of those desired by the biometrician, we may perhaps remember that they have the advantage of presenting no experimental artificiality, but of being precisely the sort which would be met in ordinary agricultural practise.

Entirely too little attention has been paid to these matters by experimentalists. Compare, for instance, some suggestions in AMER. NAT., Vol. XLV, p. 686.

allowed to become in the field, and after thoroughly drying stored until they could be studied. They were then placed in a saturated atmosphere for a few hours until the pods could be handled without snapping open, and records made of the number of pods per plant and number of ovules and seeds per pod. The seeds were then stored until thoroughly dried at laboratory temperature and humidity, when they were looked over for weighing. Particulars concerning the various characters will be given in the special sections.

D. Methods of Analysis of Data

1. Pertinent Comparisons

The possibility of an influence of ascendant starvation upon descendant characters is to be tested by a series of comparisons. The number which might be made, and with profit, is so great that space requirements impose a stringent limitation.

A first restriction is effected by basing the comparisons upon the simplest of the statistical constants.

A second limitation is effected by the exclusion of all comparisons showing the relative influence of environmental conditions on different varieties. Possibly this question will be considered in another place. Such inter-racial and inter-varietal comparisons are in this paper quite incidental to those which are strictly intra-racial and intra-varietal.

Finally the comparisons within the varieties must be limited[11] to those which seem absolutely essential to our purposes. The constants for the 40 series are given so that the reader may make any comparison he deems desirable.

In the dichotomous system adopted for these experiments, one branch of the stem material was subjected to

[11] In all we have three distinct varieties represented by 40 series of material—18 of Navy and 11 each of White Flageolet and Ne Plus Ultra. If all the $\frac{1}{2}n(n-1)$ comparisons within each variety were made for the three constants, A, σ, and CV, 789 differences and their probable errors would have to be calculated for each character observed.

starvation and the other to feeding. Both ancestral and comparison series allow of two kinds of comparisons, intra-ramal and inter-ramal.

In the first case the comparisons will be made within the same branch of the dichotomous system, *i. e.*, the offspring of the starved parents and starved grandparents will be compared with plants whose parents only were starved, both parents and grandparents being in the direct line of descent.[12]

In these tests the individuals grown on the comparison field bear to each other the relationship of "aunts" and "nieces." Such comparisons are possible where the seed retains its vitality for a number of years. They are open to criticism unless it be known that the age of the seed has no influence upon the characteristics of the plants developing from them.[13]

In the second class, the inter-ramal, are those comparisons between points on different branches of the dichotomous scheme. Here two subclasses may be recognized. In the one the comparisons are between strictly homologous points on the starved branch and on the well-fed branch. The effect of one generation's starvation will be compared with the effect of one generation's feeding. In this case comparisons will be made between "first" and "first" cousins. Or Mendelianwise, all individuals compared will be F_1, F_2 or F_n. Such comparisons will be called direct inter-ramal comparisons.

In the second subclass, the comparisons will be made between different points on the two branches; all com-

[12] In the same manner any one who desires may compare plants whose parents and grandparents were well fed with those whose parents only were well fed. This is not done here for the simple reason that I do not know that the well fed series were grown at an extreme of feeding at all comparable with the extreme of starvation which was possible in these experiments. If they were not, one would expect to find a smaller influence, if any, upon the offspring.

[13] It may have occurred to the reader that a valuable comparison for our purpose could be made within the starvation series by determining, *e. g.*, whether *USDD* whose parents *USD* had been starved, had a lower value for any character than *USD* whose parents *US* were not grown under starvation conditions. Such tests are, however, useless because both edaphic and meteorological conditions may differ from year to year.

parisons will be between ancestral individuals or their offspring belonging to different generations. Such will be called cross inter-ramal comparisons.

The most crucial test is that afforded by the direct inter-ramal comparisons. Both the intra-ramal and the cross inter-ramal comparisons have the disadvantage that the (possible) seed age factor is not excluded. Again, atmospheric (meteorological) factors play a much larger part where different seasons instead of a single season are involved.

Turning to our own available data, we note the following points concerning the comparisons:

Only such comparisons as can be made on the basis of both ancestral and comparison series are discussed, although data for some others, *e. g., NH, ND, US, FS, USC, FSC* are given.

In all cases the differences are taken

<div align="center">

Starvation

less

feeding

</div>

so that when starvation tends to reduce a character the difference bears the negative sign.

If we continue our attention strictly to those within the strain, we have the following inter-ramal comparisons:

Direct	Cross
HD–HH	*HD–HHH*
HDD–HHH	*HDD–HH*
DD–DH	*DD–DHH*
DDD–DHH	*DDD–DH*
USD–USS	*USD–USHH*
USD–USH	*USDD–USS*
USDD–USHH	*USDD–USH*
FSD–FSS	*FSDD–FSS*
FSD–FSH	*FSDD–FSH*
FSDD–FSHH	*FSDD–FSH*

If we go beyond the limits of the populations formed by splitting the seeds of the same individual into two

lots, and consider the Navy D and Navy H comparable, we get:

Direct	Cross
DD–HH	*DD–HHH*
DDD–HHH	*DDD–HH*
HD–DH	*HD–DHH*
HDD–DHH	*HDD–DH*

2. Statistical Formulæ Employed

Methods ample for all the needs of this study are furnished by the simplest of the Pearsonian statistical formulæ. The comparisons in the main are restricted to those based on the mean, standard deviation and coefficient of variation.

These do not fully describe a population, but they furnish more information concerning it than do any other three simple constants, and are sufficient for our purposes. The methods of calculation are now familiar or readily accessible to all biologists. The original data are available for any other comparison, *e. g.,* that based on skewness.

The chief possibility of untrustworthiness in the statistical constants seems to me to lie in a possible biological source of error introduced by growing the comparison series in rows instead of mixing all the individually labeled seeds together and scattering them quite at random over the entire field.[14] If because of the irregularity of the fields, some of the rows were subjected to slightly better and some to slightly poorer conditions than the average, and if the rows of an individual series were not distributed over the field in a perfectly random manner, a slight source of differentiation quite undetectible by the statistician's simple probable error would be introduced. I suspect this to be the case, and consequently our probable errors are perhaps too low *as criteria of the existence of differentiation due to the treatment of the ancestry.*

Fortunately we are not limited to a single comparison,

[14] As an extra precaution half rows were frequently used.

but have several pairs. Any one of these might be
wrong in its indication of the influence of ancestral en-
vironment because of uncontrollable factors making for
heterogeneity on the comparison tract, but as long as
these factors differ from series to series in a purely ran-
dom manner, we shall expect to get trustworthy values
by averaging the results for the several comparisons.

This averaging may be done in one or both of two ways.
Most easily one may simply note the number of alterna-
tive cases, above zero and below zero, and calculate the
probable error of either class by the formula

$$.67449 \ \sqrt{N \times .5 \times .5}$$

since, unless there be an influence of the treatment of
the ancestors, the probabilities of differences lying above
and below zero are equal. In the second case, the true
mean and standard deviation of the series of differences
may be obtained and the probable error of the mean
difference calculated by the familiar formula

$$E_m = .67449 \ \frac{\sigma}{\sqrt{N}}.$$

It only remains to say that, except when specified,
Sheppard's modification was not applied in the calcula-
tion of the moments.

III. Presentation of Data and Comparison of Constants

A. Number of Pods per Plant in Navy, White Flageolet and Ne Plus Ultra Beans

The purpose of this section is to present the data for
number of pods per plant in three varieties, represented
by 40 series and over 21,000 individuals, and to draw the
comparisons which may profitably be based upon them.
The other characters for these varieties and all of the
data for still another variety are reserved for later treat-
ment. This character, which is the most easily deter-

mined of any, is also subject to considerable possibility
of error.   It is impossible to know from an inspection of
the matured plants that some of the pods have not been
lost by accident.   Another difficulty is introduced by the
fact that some varieties of beans have a tendency to make
a '' second growth'' when they are allowed to stand in
the field after they are completely ripe.   Unless frosts
are very late these second growth pods rarely mature.
If the plants be allowed to stand in the hope that they
will ripen these second growth pods, the normal crop of
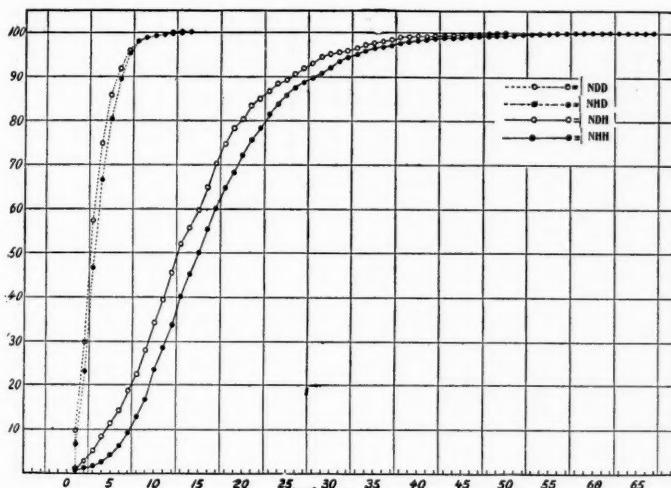
Diagram 3.   Number of pods per plant in NDD, NDH, NHD, NHH series.
All series are reduced to a percentage basis and the relative frequencies summed
from the beginning.   The influence of starvation in the reduction of the number
of pods is very conspicuous.

pods may either lose their seeds, if the weather be dry,
or decay if the weather be wet.   All that can be done is
to watch the plants carefully, to harvest as soon as prac-
tically all the pods that are ripe, and to pull off any sec-
ond growth sprouts.   This apparently introduces a con-
siderable personal equation into the work, but even if true
it is unavoidable.   I do not believe that a palpable source
of error was introduced since (*a*) a large proportion of
the plants do not show the second growth at all; (*b*) when

they do, a person with a little practise will make very few mistakes; (*c*) even if errors are made, the treatment is the same for all series.

All the pods counted had at least one matured seed. This specification is necessary since, especially in the autumn, some plants produce quite a number of half developed and completely sterile pods. If these were included there would be no point where a line could be

WHITE FLAGEOLET
FSD AND FSH

STARVED, 1908

FED, 1908

NE PLUS ULTRA
USD AND USH

STARVED, 1908

FED, 1908

0   10   20   30   40   50

0   10   20   30   40
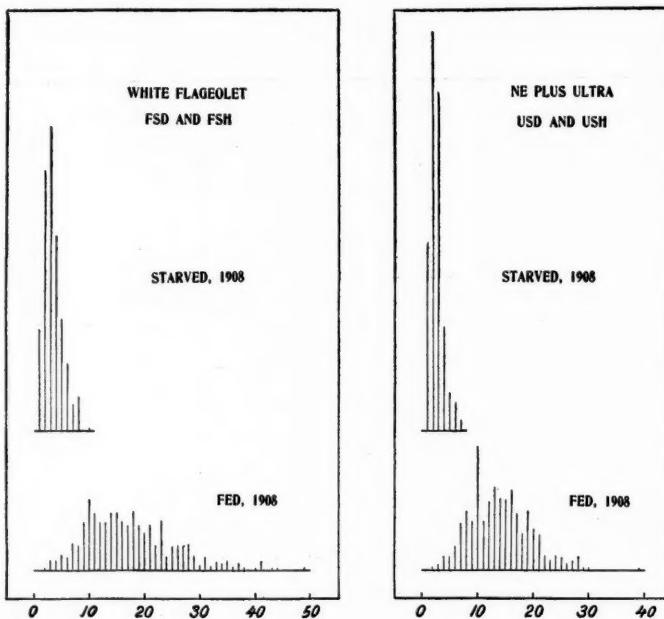
Diagrams 4 and 5. Percentage frequency of number of pods per plant under starvation and feeding conditions for White Flageolet and Ne Plus Ultra series, 1908.

drawn between the number of flowers and the number of pods produced by an individual.

The record forms do not interest the general reader.

The original data are given in Tables *A–C*. The physical constants appear in Tables I–III.

The extreme sensitiveness of the number of pods per plant to environmental conditions is seen at once from an

inspection of the tables of raw data, and better still from the three graphs, diagrams 3–5, for the number of pods per plant in the 1908 series.[15]

We may now summarize as briefly as possible, and largely by diagrams, the results which may be gathered

TABLE I

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
NH	15.2375 ± .4042	7.5800 ± .2858	49.746 ± 2.294
NHH	16.9919 ± .1518	8.6696 ± .1073	51.022 ± 0.781
NHHH	11.9308 ± .0977	5.1652 ± .0691	43.293 ± 0.679
NHD	3.9682 ± .0348	1.9433 ± .0246	48.972 ± 0.755
NHDD	4.5822 ± .0462	2.3756 ± .0327	51.844 ± 0.884
ND	2.6782 ± .0335	1.1662 ± .0237	43.545 ± 1.040
NDD	3.5926 ± .0563	1.8917 ± .0398	52.657 ± 1.384
NDDD	4.4074 ± .0608	1.9329 ± .0430	43.855 ± 1.149
NDH	14.6179 ± .2148	8.2422 ± .1519	56.385 ± 1.330
NDHH	11.8265 ± .1408	4.9595 ± .0995	41.935 ± 0.978
NHHC	11.9597 ± .2212	7.3010 ± .1564	61.047 ± 1.728
NHHHC	10.6498 ± .1788	6.2390 ± .1264	58.583 ± 1.541
NHDC	10.9362 ± .2747	7.8970 ± .1943	72.210 ± 2.539
NHDDC	10.2851 ± .1845	6.1042 ± .1305	59.350 ± 1.656
NDDC	9.3098 ± .2259	5.3470 ± .1597	57.434 ± 2.210
NDDDC	9.9819 ± .2360	6.3673 ± .1669	63.789 ± 2.252
NDHC	9.9801 ± .2079	6.5532 ± .1470	65.662 ± 2.010
NDHHC	9.9851 ± .1827	6.2839 ± .1292	62.933 ± 1.732

TABLE II

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
USS	15.7382 ± .1562	6.0379 ± .1104	38.365 ± 0.798
USH	14.0416 ± .1972	5.5542 ± .1394	39.555 ± 1.138
USHH	8.4375 ± .1462	3.2439 ± .1034	38.446 ± 1.250
USD	2.5929 ± .0468	1.2265 ± .0331	47.300 ± 1.536
USDD	3.6203 ± .0919	2.0986 ± .0650	57.970 ± 2.322
USC	10.1434 ± .1285	4.3846 ± .0908	43.226 ± 1.050
USSC	11.7068 ± .1594	4.6188 ± .1127	39.454 ± 1.102
USHC	9.9844 ± .1541	4.0936 ± .1090	41.000 ± 1.262
USHHC	10.1103 ± .1564	4.6299 ± .1106	45.794 ± 1.303
USDC	8.4474 ± .1331	3.8477 ± .0942	45.549 ± 1.326
USDDC	10.1231 ± .1426	3.8579 ± .1008	38.110 ± 1.132

[15] The 1908 instead of the 1907 series was chosen for these graphical comparisons, since the number of available series is larger—eight as compared with two—and since the number of individuals is much greater, giving much smoother results. The data are available for any similar comparison the reader may care to make. To render the results for all series quite comparable, they have been reduced to a percentage basis. In the first diagram, where data for four series are laid side by side, the percentages have been summed from the beginning for each pod class. In the second and third diagram the percentage frequency of each number of pods per plant is represented by the height of a line.

TABLE III

Series	Mean and Probable Error	Standard Deviation and Probable Error	Coefficient of Variation and Probable Error
FSS	15.0265 ± .1697	7.4134 ± .1200	49.335 ± 0.974
FSH	17.2947 ± .2456	7.9364 ± .1736	45.889 ± 1.197
FSHH	11.8415 ± .1562	4.7959 ± .1104	40.501 ± 1.075
FSD	3.4252 ± .0552	1.6929 ± .0390	49.424 ± 1.390
FSDD	4.0362 ± .0593	1.7294 ± .0419	42.848 ± 1.215
FSC	14.2218 ± .2056	7.3804 ± .1454	51.895 ± 1.268
FSSC	12.9562 ± .1856	6.1678 ± .1313	47.605 ± 1.222
FSHC	12.2431 ± .2068	6.3729 ± .1463	52.053 ± 1.483
FSHHC	14.1505 ± .2115	7.9996 ± .1495	56.532 ± 1.353
FSDC	12.9055 ± .2616	6.7949 ± .1850	52.652 ± 1.787
FSDDC	14.4981 ± .2090	7.1885 ± .1478	49.583 ± 1.245

from the tables of constants. As already emphasized the comparisons between the ancestral series are of interest for our present purposes only in so far as they furnish proof that the parents of the comparison series were conspicuously differentiated in type and variability because of the environmental conditions to which they were subjected. The reader must always keep in the foreground the fact that our problem is not to determine in detail what the causes of this differentiation are, but merely to show that a conspicuous differentiation exists and to ascertain whether it has any weight in determining the characteristics of the offspring.

The differences between the starved and well-fed ancestral series are so well marked that constants are best represented by graphs for all the series. In diagrams 6 and 7, which embody data for all possible comparisons for A and σ, roughly made, the key number of the variety is given along the left-hand margin. The value of the constant for the ancestral series is indicated by the position of a solid dot when the series is a starved one, and by the position of a circle when it is a well-fed one. The value of the constant for the offspring of each of these ancestral series grown upon the comparison field is shown by the position of a solid square under a separate scale. Thus the key to the comparison series is given by adding C to the formula for the ancestral series.

The graphs for the mean number of pods per plant and for the standard deviation of number of pods per plant

brings out with great force and clearness the following facts:

(*a*) The difference between the ancestral series subjected to the *S* and *H* conditions and those subjected to the *D* environment is very great.   In all cases means and
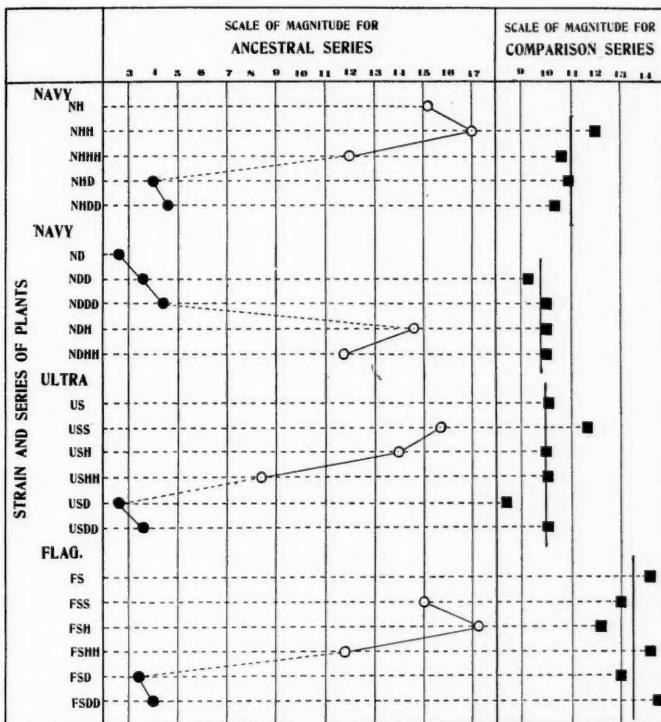

Diagram 6.   Mean number of pods per plant in ancestral, or ascendant, series subjected to various conditions of starvation and feeding and in the offspring, descendant, or comparison series subjected to conditions uniform for each strain. Note that the means for the ancestral series vary widely and in direct response to environmental conditions.   The comparison series, however, show much smaller differences, and no clear indications of an influence of the ancestral conditions.

standard deviations are conspicuously higher when the plants are well fed than when they are starved.

(*b*) There are considerable differences between a strain grown on the same field in different years.

Season is evidently a large factor in determining number of pods per plant. This is most striking in the means but it is also detectible in the standard deviations. For the means we note that in each of the four strains the average was conspicuously lower in 1909 than in 1908 on the H field and slightly higher in 1909 than in 1908 on the
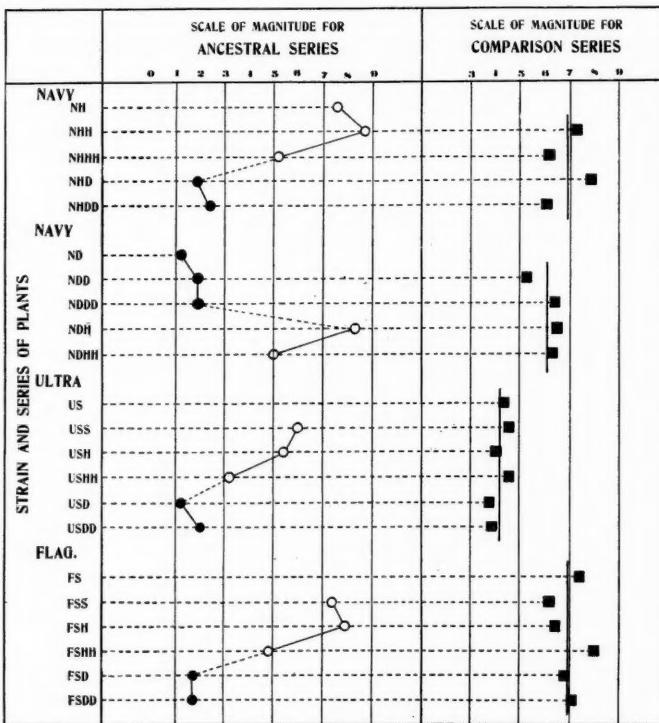
Diagram 7. Standard deviation of number of pods per plant in ancestral and comparison series. Compare the explanation of diagram 6.

D field. The standard deviations show precisely the same results for the H field, but the differences between 1908 and 1909 for the D crops are relatively small.

(c) The differences between the comparison series are considerable, but it is impossible to be certain of any influence of the treatment of the ancestors.

(*a*) and (*b*) are facts to be expected from the common experience of all those who have occupied themselves extensively with the growing of plants; they are summarized here merely because it is idle to discuss (*c*) unless the results for (*a*) are clean cut.[16]

Turn now from diagrams to physical constants. Consider first the intra-ramal comparisons, those cases in which individuals whose ancestors have been starved for a longer period are contrasted with individuals in the same line of descent whose ancestors have been starved for a shorter period of time. The necessary constants appear in Table IV.

TABLE IV

Description of Material	Ancestors Starved for Two Generations	Ancestors Starved for Three Generations
Ancestors starved for one generation:		
USDC series:	*USDDC* series:	
Mean..........................	$+\ 1.6757\ \pm\ 0.1952$	
Standard deviation.............	$+\ 0.0102\ \pm\ 0.1378$	
Coefficient of variation..........	$-\ 7.439\ \ \ \pm\ 1.743$	
FSDC series:	*FSDDC* series:	
Mean..........................	$+\ 1.5926\ \pm\ 0.3348$	
Standard deviation.............	$+\ 0.3936\ \pm\ 0.2369$	
Coefficient of variation..........	$-\ 3.069\ \ \ \pm\ 1.178$	
NHDC series:	*NHDDC* series:	
Mean..........................	$-\ 0.6511\ \pm\ 0.3309$	
Standard deviation.............	$-\ 1.7928\ \pm\ 0.2341$	
Coefficient of variation..........	$-12.960\ \ \ \ \pm\ 3.031$	
Ancestors starved for two generations:		
NDDC series:		*NDDDC* series:
Mean..........................		$+\ 0.6721\ \pm\ 0.3266$
Standard deviation.............		$+\ 0.9203\ \pm\ 0.2311$
Coefficient of variation..........		$+\ 6.355\ \ \ \pm\ 3.155$

Two of these means seem to be significant in comparison with their probable errors, and both of these indicate that starvation of the ancestry for two as compared with one generation, increases the number of pods on the offspring plant. But, it must be remembered that the seed is necessarily a year older for a single generation of starvation only. Furthermore, the series are too few and the differences are entirely too small—only 1.6 pods —to lay particular stress upon it.

The second set of comparisons, the inter-ramal, those

[16] Those noted under (*b*) may be treated more fully later.

between individuals whose ancestors had been subjected to distinctly unlike treatment is made in Tables V–VIII.

Consider first the means. Altogether there are 28 inter-ramal comparisons, direct and cross. The number of pods is smaller in the plants whose ancestors had been starved in 16 out of 28 cases. If there were no relationship between the conditions to which the ancestors were subjected and the number of pods which their offspring produced, one would expect 14 to be negative, providing the errors of random sampling had not to be allowed for. But the probable error is

$$.6745\sqrt{28 \times .5 \times .5} = 1.79.$$

Clearly a difference of 2 ± 1.79 has no significance.

If now we restrict the comparison to differences significant with regard to their probable errors, and consider Diff./$E_{\text{diff.}} > 3$ to be significant, we note that only 11 out of the 28 differences may be regarded as statistically trustworthy. Of these, 9 have the negative and only 2 the positive sign. Certainly this looks as though there were a very slight effect of the starvation of the ancestors, but nevertheless an effect quite detectible by the statistical methods.

This point may be tested further by taking the averages, regarding sign, of the pertinent differences for the series of the three varieties. To make sure that slight racial differences between ND and NH do not obscure the results we recognize two classes of comparisons, within the strain and between strains. The results are:

$$\begin{aligned}
\text{Navy, Within Strains,} \quad A &= - .515\\
\text{Between Strains,} \quad A &= - .515\\
\text{General Average,} \quad A &= - .515\\
\text{Ne Plus Ultra,} \qquad\qquad A &= -1.315\\
\text{White Flageolet,} \qquad\quad A &= + .585
\end{aligned}$$

In all cases except the White Flageolet series[17] the number of pods is slightly lower when the ancestors have been starved.

[17] Note also that the two cases of significantly positive differences occur in the White Flageolet variety.

TABLE V

Description of Material	Ancestors Starved for One Generation NHDC	Ancestors Starved for Two Generations NHDDC
Ancestors well fed for one generation: NDHC series:		
Mean..........................	$+ 0.9561 \pm 0.3445$	$+ 0.3050 \pm 0.2780$
Standard deviation.............	$+ 1.3438 \pm 0.2437$	$+ 0.4490 \pm 0.1965$
Coefficient of variation..........	$+ 6.548 \pm 3.238$	$- 6.312 \pm 2.604$
Ancestors well fed for two generations: NHHC series:		
Mean..........................	$- 1.0235 \pm 0.3527$	$- 1.6746 \pm 0.2881$
Standard deviation.............	$+ 0.5960 \pm 0.2494$	$- 1.1968 \pm 0.2037$
Coefficient of variation..........	$+11.163 \pm 3.071$	$- 1.697 \pm 2.393$
NDHHC series:		
Mean..........................	$+ 0.9511 \pm 0.3298$	$+ 0.3000 \pm 0.2596$
Standard deviation.............	$+ 1.6131 \pm 0.2332$	$- 0.1797 \pm 0.1836$
Coefficient of variation..........	$+ 9.277 \pm 3.073$	$- 3.583 \pm 2.396$
Ancestors well fed for three generations: NHHHC series:		
Mean..........................	$+ 0.2864 \pm 0.3277$	$- 0.3647 \pm 0.2569$
Standard deviation.............	$+ 1.6580 \pm 0.2319$	$- 0.1348 \pm 0.1817$
Coefficient of variation..........	$+ 13.627 \pm 2.970$	$+ 0.767 \pm 2.262$

TABLE VI

Description of Material	Ancestors Starved for Two Generations NDDC	Ancestors Starved for Three Generations NDDDC
Ancestors well fed for one generation: NDHC series:		
Mean..........................	$- 0.6703 \pm 0.3071$	$+ 0.0018 \pm 0.3145$
Standard deviation.............	$- 1.2062 \pm 0.2170$	$- 0.1859 \pm 0.2225$
Coefficient of variation..........	$- 8.228 \pm 2.987$	$- 1.873 \pm 3.019$
Ancestors well fed for two generations: NHHC series:		
Mean..........................	$- 2.6499 \pm 0.3162$	$- 1.9778 \pm 0.3234$
Standard deviation.............	$- 1.9540 \pm 0.2236$	$- 0.9337 \pm 0.2287$
Coefficient of variation..........	$- 3.613 \pm 2.805$	$+ 2.742 \pm 2.838$
NDHHC series:		
Mean..........................	$- 0.6753 \pm 0.2905$	$- 0.0032 \pm 0.2985$
Standard deviation.............	$- 0.9369 \pm 0.2054$	$+ 0.0834 \pm 0.2110$
Coefficient of variation..........	$- 5.499 \pm 2.807$	$+ 0.856 \pm 2.841$
Ancestors well fed for three generations: NHHHC series:		
Mean..........................	$- 1.3400 \pm 0.2881$	$- 0.6679 \pm 0.2961$
Standard deviation.............	$- 0.8920 \pm 0.2037$	$+ 0.1283 \pm 0.2093$
Coefficient of variation........	$- 1.149 \pm 2.694$	$+ 5.206 \pm 2.729$

Consider now only the ten direct inter-ramal and the ten cross inter-ramal, forming the twenty possible intra-varietal comparisons. Of the ten direct intra-ramal comparisons which are available from the four series, seven have the negative and three the positive sign. In two cases only is Diff./$E_{diff.}$ > 3, and in one case > 2.5.

TABLE VII

Description of Material	Ancestors Starved for One Generation USDC	Ancestors Starved for Two Generations USDDC
Ancestors well fed for one generation:		
USSC series:		
Mean..........................	− 3.2594 ± 0.2076	− 1.5837 ± 0.2138
Standard deviation............	− 0.7711 ± 0.1470	− 0.7609 ± 0.1513
Coefficient of variation.........	+ 6.095 ± 1.724	− 1.344 ± 1.579
USHC series:		
Mean..........................	− 1.5370 ± 0.2037	+ 0.1387 ± 0.2100
Standard deviation............	− 0.2459 ± 0.1442	− 0.2357 ± 0.1483
Coefficient of variation.........	+ 4.549 ± 1.830	− 2.890 ± 1.695
Ancestors well fed for two generations:		
USHHC series:		
Mean..........................	− 1.6629 ± 0.2054	+ 0.0128 ± 0.2117
Standard deviation............	− 0.7822 ± 0.1453	− 0.7720 ± 0.1497
Coefficient of variation.........	− 0.245 ± 1.859	− 7.684 ± 1.726

TABLE VIII

Description of Material	Ancestors Starved for One Generation FSDC	Ancestors Starved for Two Generations FSDDC
Ancestors well fed for one generation:		
FSSC series:		
Mean..........................	− 0.0507 ± 0.3208	+ 1.5419 ± 0.2795
Standard deviation............	+ 0.6271 ± 0.2269	+ 1.0207 ± 0.1977
Coefficient of variation.........	+ 5.047 ± 2.165	+ 1.978 ± 1.744
FSHC series:		
Mean..........................	+ 0.6624 ± 0.3335	+ 2.2550 ± 0.2939
Standard deviation............	+ 0.4220 ± 0.2358	+ 0.8156 ± 0.2078
Coefficient of variation.........	+ 0.599 ± 2.322	− 2.470 ± 1.936
Ancestors well fed for two generations:		
FSHHC series:		
Mean..........................	− 1.2450 ± 0.3365	+ 0.3476 ± 0.2973
Standard deviation............	− 1.2047 ± 0.2379	− 0.8111 ± 0.2102
Coefficient of variation.........	− 3.880 ± 2.241	− 6.949 ± 1.838

All these are negative. There are no statistically signifi-
cant positive differences, the actual values being .013
± .212, .348 ± .297, and .662 ± .334. The two larger of
these occur in the White Flageolet series. The mean for
the ten direct comparisons is — .589 pods.

Of the ten cross inter-ramal comparisons, five are neg-
ative and five are positive; six are significant with regard
to their probable error, four with the negative and two
with the positive sign. In both cases of positive differ-
ences (*i. e.,* where the seeds from starved ancestors pro-
duced more pods than those from fed ancestors) the seed
from the fed plants was a year older than that from the
starved plants. The average for the cross comparisons
is — .262 pods.

Consider the standard deviations.

As already noted, and as is clearly to be seen from the graph, the standard deviations for the starved and fed ancestral series show differences agreeing in general with those seen in the means. This is to be expected, since A and σ are generally closely correlated. For this reason it is idle to discuss the influence of starvation or feeding upon variability on the basis of the standard deviation alone.

Turning to the comparison series, we note that of the 28 differences, taken altogether, 17 are negative and 11 positive. The deviation from expectation is therefore 3 ± 1.79, and can not be asserted to be significant.

Again taking Diff./$E_{\text{diff.}} > 3$ as indicating differences significant with regard to the errors of sampling, we note that 17 cases out of 28 are statistically significant. Of these 17 cases, 12 are negative and 5 are positive. Consider averages as before:

$$
\begin{aligned}
\text{Navy, Within Strains, } & A = -.165 \\
\text{Between Strains, } & A = -.053 \\
\text{General Average, } & A = -.109 \\
\text{Ne Plus Ultra, } & A = -.595 \\
\text{White Flageolet, } & A = +.145
\end{aligned}
$$

Again limiting comparisons to the strictly intravarietal, and segregating into direct and cross interramal comparisons, we find that of the ten direct comparisons possible in the four lots, six are negative and four positive in the sign of the difference. Only four are statistically significant, i. e., Diff./$E_{\text{diff.}} > 3$, and all are negative. The average is $-.221$. Of the ten cross interramal comparisons, seven are negative and three are positive in sign; with regard to their probable error, eight are significant; of these five are negative and three are positive. The mean for the series is $-.181$.

Note the following points concerning the relative variabilities as expressed by the coefficients of variation.

Taken altogether, fifteen differences are negative and thirteen are positive in sign. Accepting a difference of

three times its probable error as statistically significant, we note that altogether only six out of the twenty-eight differences may be regarded as trustworthy. Of these four are positive and two are negative in sign. Taking means as for the two preceding constants, we find:

Navy, Within Strains, $A = + .912$
Between Strains, $A = + .912$
General Average, $A = + .912$
Ne Plus Ultra, $A = - .253$
White Flageolet, $A = - .946$

With mean differences as slight as these, one certainly can not argue that the starvation of the parents has had any pronounced influence upon the relative variability of the offspring.

Provisional Summary

1. The foregoing pages are devoted to a statement of problems, description of methods and the presentation of a first part of the data secured in a biometric investigation of the influence of the starvation of the ascendants upon the characteristics of the descendants in garden beans. Since several months will necessarily elapse before all of the materials can be worked up, it has seemed undesirable to withhold the constants already calculated and checked, viz., those for number of pods per plant in three varieties represented by forty series comprising altogether about 21,000 individuals. The publication is therefore partial but in no sense preliminary. Several questions that might be discussed on the basis of the data presented are passed over until more series of material can be lined up. The conclusions drawn—even for number of pods per plant—are provisional merely.

2. The purpose of this research was not to ascertain the physico-chemical factors to which starvation is due, but to determine whether such artificial depauperization of the ancestors has any influence upon the characters of the offspring. Such ordinary ''fertile'' and ''sterile'' or ''good'' and ''poor'' agricultural land was therefore

taken for the ancestral series as would produce moderately extreme conditions of depauperization and luxuriance in the crops.

3. The influence of from one to three generations starvation of the ascendants upon the characteristics of the adult descendants is not conspicuous, in fact hardly to be detected by the eye in the field. Statistical constants *seem*, however, to show a slight yet unmistakable influence of the treatment of the ancestors in the form of a slight decrease in the number of pods per plant.

4. The published data are as yet insufficient to justify any discussion of the question of the cumulative influence of the starvation conditions, or of the mechanism through which the characters of the offspring plants are modified. Evidence on these and various other pertinent questions are being gathered as rapidly as possible.

MENDELIAN PROPORTIONS AND THE INCREASE OF RECESSIVES

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RECENTLY in working over some data[1] on the inheritance of lefthandedness, certain questions came up, which seem of considerable interest, as: Does the proportion of lefthanded people remain the same from century to century or does it diminish or increase? In any case, how does the result come about? Although well aware of the present-day aversion to arm-chair biology, it yet seems that these problems can hardly be attacked from the experimental side, and that a theoretical discussion may be of some value.

It may be stated at the outset that I consider lefthandedness to be a true Mendelian recessive,[2] and also that there is no selective mating with reference to the character. There seems also no reason to suspect that lefthanded people exhibit less fertility[3] than normal individuals. If these suppositions are correct, the condition offers a happy opportunity for study, since most human characters thus far examined are such as might be likely to be affected by selection.

Concerning the first question asked above, no positive answer can be given, for there are no statistics. It is probable that the affection is a very old one, and not of recent origin. If it tends to increase it might be expected that a very considerable part of the population would now show the condition, while if it is decreasing, we

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[1] As yet unpublished.

[2] Evidence for this view is shown by Professor H. E. Jordan in the *Breeders' Magazine,* Vol. II, pp. 19–29 and 113–124. My own observations confirm this belief.

[3] My own records even suggest the opposite condition, but this is probably merely chance due to the small numbers studied.

should, after all the long period of its existence, find
only a few persons with the condition.

On the "presence and absence" theory lefthandedness
is due to the loss or "dropping out" of the factor or de-
terminer for righthandedness. If such loss could occur
in the past, why not from time to time now? If so, why
would not the proportion of lefthanded people continu-
ally increase?

In a population where the dominant, the heterozygote
and the recessive have a certain proportion, slight
changes in the relative numbers seem to have no perma-
nent effect. There is a tendency to stability and unless
a certain point is passed because of the appearance of an
unusual number of recessives, there will be a return to
the usual ratio. The mathematical features of the case
have been discussed by Dr. W. J. Spillman,[4] and by Mr.
G. H. Hardy.[5] The earliest clear statement of the case
which I have seen is by Dr. George H. Shull[6] in his dis-
cussion of elementary species in *Bursa bursa-pastoris.*

The fact of the stability of certain ratios and instabil-
ity of others can be readily comprehended from the fol-
lowing tables (I, II, III). We may let RR represent a
pure righthanded individual, Rr, a heterozygous right-
handed individual, and rr, a lefthanded individual. As
a first example it may be supposed that a large popula-
tion exists in which the various types occur in the fol-
lowing proportions, viz.:

1 pure righthanded: 2 heterozygous righthanded:

1 lefthanded, or,

$$RR:2Rr:rr.$$

Random matings would occur in such fashion that mem-
bers of each group would mate with those of their own
group or with members of other groups. The various
possibilities are represented in Table I. The filial gen-

[4] *Science*, N. S., Vol. XXVIII, pp. 252–254, 1908.

[5] *Ibid.*, pp. 49, 50.

[6] *Science*, N. S., Vol. XXV, pp. 590, 591, 1907.

eration derived in Table I is composed of the three types in the same ratio as in the parental generation.[7]

TABLE I

MATINGS AND OFFSPRING IN A LARGE POPULATION HAVING THE COMPOSITION 1 RIGHTHANDED: 2 HETEROZYGOUS RIGHTHANDED: 1 LEFTHANDED (*RR* : 2*Rr* : *rr*)

Matings	Offspring		
	RR	*Rr*	*rr*
RR × *RR*	1		
RR × 2*Rr*	1	1	
RR × *rr*		1	
2*Rr* × *RR*	1	1	
2*Rr* × 2*Rr*	1	2	1
2*Rr* × *rr*		1	1
rr × *RR*		1	
rr × 2*Rr*		1	1
rr × *rr*			1
Totals	4	8	4
or	1	2	1

As a second example, the ratio 2:2:2 may be taken. This will give the results shown in Table II. The ratio 2:2:2 is not constant, but stability is reached in F_1, which is found to show the same ratio as our previous case, viz., 1:2:1.

TABLE II

MATINGS AND OFFSPRING IN A LARGE POPULATION HAVING THE PROPORTION 2 RIGHTHANDED: 2 HETEROZYGOUS RIGHTHANDED: 2 LEFTHANDED (2*RR* : 2*Rr* : 2*rr*)

Matings	Offspring		
	RR	*Rr*	*rr*
2*RR* × 2*RR*	4		
2*RR* × 2*Rr*	2	2	
2*RR* × 2*rr*		4	
2*Rr* × 2*RR*	2	2	
2*Rr* × 2*Rr*	1	2	1
2*Rr* × 2*rr*		2	2
2*rr* × 2*RR*		4	
2*rr* × 2*Rr*		2	2
2*rr* × 2*rr*			4
Totals	9	18	9
or	1	2	1

[7] I am indebted to my colleague, Professor Saul Epsteen, of the Department of Mathematics, for checking my method of analysis.

In Table III a few possible matings are shown with the percentage of recessives and the constant ratios which appear in the next generation. It is apparent from examination of the figures that if a disturbance takes place there is often a partial return in the next generation to the original condition. Sometimes this return is complete, as would occur if, beginning with the ratio of $1:2:1$, some disturbance should make it $1:1:1$. In the next generation there would be a return to the $1:2:1$ condition. There were 25 per cent. of recessives at the beginning. This became changed to 33.3 per cent. by mutation but returned in the next generation to 25 per cent.

TABLE III

EXAMPLES OF RATIOS OF DOMINANTS, HETEROZYGOTES AND RECESSIVES, TOGETHER WITH THE CONSTANT RATIOS DERIVED IN THE FIRST FILIAL GENERATION. THE CONSTANT RATIOS ALL HAVE THE FORM $A^2 + 2AB + B^2$

Original Ratio	Per Cent. Recessives	Constant Ratio in F_1	Per Cent. Recessives
$1:1:1$	33.3	$1: 2: 1$	25.0
$1:1:2$	50.0	$9:30:25$	39.0
$1:1:4$	66.6	$1: 6: 9$	56.2
$1:2:1$	25.0	Constant	Constant
$1:3:1$	20.0	$1: 2: 1$	25.0
$1:3:2$	33.3	$25:70:49$	34.0
$1:4:4$	44.4	Constant	Constant
$2:1:2$	40.0	$1: 2: 1$	25.0
$4:4:1$	11.1	Constant	Constant
$4:6:1$	9.0	$49:56:16$	13.2

But there is not always a diminution of this kind. If the original ratio be $4:4:1$, which is constant, and this be changed by mutation to $4:6:1$, the original 11.1 per cent. of recessives is at first reduced to 9 per cent., only to rise in succeeding generations to 13.2 per cent. It is very easy to overestimate the importance of the tendency to return to a stable ratio, since such stable ratios are practically without limit, and instead of returning to the same ratios, it is easily possible to reach stability in a new ratio somewhat different from the original. This may be shown by an example (Table IV).

TABLE IV

Figures Showing the Formation of a New Stable Ratio in a Popula-
tion having at First the Composition 4 : 4 : 1 when a Small
Number of Heterozygotes become Recessives through Mutation

Ratio in the original population: 400 : 400 : 100 = 11.1 per cent. recessive.
Ratio after mutation: 400 : 396 : 104 = 11.5 per cent. recessive.
Ratio of the next generation:
          89,401 : 90,298 : 22,801 = 11.2 per cent. recessive.

The change in any case is not so simple as mathemat-
ical study would at first suggest, for many of the indi-
viduals mate with members of earlier or later genera-
tions. When a considerable number of recessive mutants
appear in a given generation this excess is, in part, re-
duced by matings with members of the normal genera-
tions before and after them. Hence a return to the nor-
mal or usual condition is made easy. These considera-
tions naturally suggest a reason for the comparative
stability of species within a genus or of elementary
species within a Linnæan species.

From what has been said it will be seen that unless a
recessive character is arising by mutation at some ap-
preciable rate there will be little or no increase in the
proportion of individuals exhibiting this character. On
the other hand, whenever a considerable number of mu-
tants do appear the normal condition of equilibrium is
disturbed and a new stable ratio becomes established in
which the recessives are in larger proportion.

There are probably many recessive characters which
are not the objects of natural selection by the environ-
ment nor of sexual selection in mating. Lefthandedness
may well be such a character. It certainly seems that
the proportion of individuals with such characters will
increase slowly through long periods of time. Let it be
supposed, for example, that the proportion of dominants,
heterozygotes and recessives in the general population
is 9 : 6 : 1. Now it is probably far easier in mutation for
a given factor to drop out than to be added. If, however,
the dropping out and addition could take place with

equal facility, there would still be much in favor of the recessive. In the supposed ratio $9:6:1$ it is possible for any one of the dominants or heterozygotes to lose a determiner. In other words, on the average fifteen out of sixteen individuals have an opportunity to vary toward lefthandedness; that is, 93.9 per cent. On the other hand, only the heterozygotes and the recessive can vary toward righthandedness; seven out of sixteen, therefore, have this possibility, or 43.7 per cent. of the population. If, therefore, the addition of the factor were as easily accomplished as the loss of the factor—which is probably never true—loss of a factor would be more than twice as likely to occur as gain. With the ratio $1:2:1$ opportunities are of course equal for upward and downward mutation. In a population with more than 25 per cent. of recessives, the number of heterozygotes plus recessives is greater than the number of heterozygotes plus dominants, as, for example, with the ratio $1:4:4$, in which the recessives make up 44.4 per cent. of the population.

It would seem from the above that there is a constant tendency for the proportion of individuals showing non-important recessive characters to increase, unless indeed mutative changes occur so slowly that the population is constantly held back to a stable ratio. We are led naturally to the thought that for species in general the individuals showing recessive mutations may be expected to increase at the expense of the original type, unless the characters lost are of some real importance to existence or to mating. Just this sort of thing has probably taken place with the shepherd's purse, *Bursa bursa-pastoris*. It can hardly be doubted that the numerous species described by Almquist[8] are derived from a single original species. If the total number of *Bursas* in the world remains the same from century to century and these elementary species appear in some number from time to

[8] Noted by Dr. George Harrison Shull, ''Advance Print from the Proceedings of the Seventh International Zoological Congress, Boston Meeting, 1907.''

time, they must be crowding upon the original form. Other examples in great number will occur to any one. Thus there can be little doubt that primitive man was dark-skinned and dark-eyed. The various modern races were produced—so far as skin-color and eye-color are concerned—by dropping out the factors (determiners) for these characters. In our own Caucasian race, it seems not unreasonable to suppose that we are tending toward a condition of blondness, for there seems to be no natural or sexual selection against this character.[9]

I am not unmindful of the fact that an apparently unimportant character such as righthandedness may be bound up with other characters of great consequence. In such case lefthandedness might mean, for example, a distinct inferiority in metabolic activity.[10] Unless the recessiveness is associated with weakened nutrition or other enfeebled condition, it would seem most natural for elementary species, when once originated, to increase in number of individuals by continued mutation.

Dr. Shull points out in his paper previously cited on "Elementary Species and Hybrids of *Bursa*" that recessive mutants may have an advantage over dominant mutants if fluctuating conditions tend to eliminate now one form, now the other. The killing off of dominant mutants may be easily accomplished, but this is not the case with recessives.[11] This is perhaps only another way of stating the well-known fact that it is hard in plant or animal

[9] The claim that light-skinned and light-eyed people are not adapted to sunny climates seems hardly substantiated.

[10] Cf. the observations by Professor Thomas Hunt Morgan upon mutants of the fruit fly, *Drosophila*, in the *Journal of Experimental Zoology*, Vol. XI, p. 408, 1911.

[11] To use his own words: "The recessive mutant may be preserved indefinitely under the protection of the dominant characteristics of its more successful parent. Such prolongation of the life of a recessive may serve to tide it over times of special stress or may continue its existence until the various distributing agents have carried it beyond the limits of the habitat in which it is a failure into others in which it may become a success." This same idea has been suggested by my colleague, Professor T. D. A. Cockerell, in a conversation regarding the general question of increase of recessives.

breeding to get rid of recessive characters which are not wanted.

Summary

In the foregoing discussion an attempt has been made to exhibit clearly the facts of stable ratios involving Mendelian dominants, heterozygotes and recessives. While suggested by a study of lefthandedness, what has been said will apply to any recessive character which is not selected against in mating and which does not affect the success of the organism in other ways. I have tried to accord full value to the mathematical features of the case, and have pointed out the various checks which tend to hold the population in a given ratio. Yet I have been unable to escape the conclusion that recessive mutants, unless inherently weak in some respect, must tend to increase in numbers at the expense of original dominant types. These conclusions are reached from a consideration of the following points: (1) The greater ease with which characters may be lost than gained. (2) The great number of combined dominants and heterozygotes which through mutation may reach a simpler condition as compared with the small number of recessives and heterozygotes which may be imagined as affording opportunity for mutation to dominance.[12] (3) The more likely survival of recessives in an environment of changing conditions in which now the dominant and now the recessive is hard pressed to maintain its existence.

[12] Unless the ratio of the three types is $1 : 2 : 1$, when the opportunities are the same in each direction.

THE INCONSTANCY OF UNIT–CHARACTERS[1]

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THERE can be no reasonable doubt that Mendel's law is of fundamental importance in genetics. It explains so many of the anomalous facts and seeming contradictions encountered in practical breeding. The basic fact underlying this law is the existence of unit-characters, independently inherited. Their independence makes it possible to combine them in any desired way through the agency of cross-breeding.

In the first flush of enthusiasm over the rediscovery of Mendel's law it was thought by some that recombination of unit-characters through crossing was to solve all the problems of breeding relating to the production of new and improved varieties. But experienced animal breeders have, as a rule, been very conservative in their expectations, a conservatism justified by the knowledge of how painfully slow and tedious is the process of improving a breed in any essential regard. For though it is easy enough in two generations to get new color varieties by crossing breeds of different color, the new creations will, in respects other than color, not be the same as either of the breeds crossed; they may be inferior to both in every respect but color, and it will be a difficult, if not impossible, task to restore the desirable qualities lost. The reason is that our improved breeds differ from each other in so many minor characteristics that it is quite impossible to give attention to all of them simultaneously. For as the number of variable characters resulting from a cross increases, a particular combination of characters will become more rare in occurrence and harder to fix.

Soon after it was discovered that unit-characters exist,

[1] An address delivered at the University of Illinois, April 19, 1912.

the question was raised whether they are or are not constant.

In our descriptions we call these characters A, B, C, etc., and the recombinations are AB, BC, AC, etc. In our formulæ A is always A, and B is always B, but it is an open question whether in our living animals the characteristics or qualities designated by these symbols are from generation to generation as constant and changeless as the symbols. Bateson and Johannsen and Jennings have assumed that they are, that a horn is always a horn, and a toe a toe. When it is pointed out that horns are not all alike, that they differ in size, shape and color, the reply is made that these differences are due to *other things*, that is, that these are independent qualities not inherent in the horn itself. Now there is force in this argument because we know that a particular color can be dissociated from the horn, why not also size and shape? Nevertheless if we dissociate from the horn *all* color, size and shape we shall have no horn left. The real unit-characters, therefore, which we can think of in a concrete way and deal with in actual breeding operations are differences in *degree* of horn-development, in length, thickness, curvature or coloration. Who shall say whether these differences are few or many? We can conceive of an infinite number of gradations in size, shape and color between known extremes and it is difficult to believe that any one of these is impossible of realization. Nevertheless an important body of present-day naturalists, those who with De Vries believe in mutation, would have us think that these minor gradations are not heritable. Their reasoning is as follows. Suppose we cross horned with hornless cattle. All the immediate offspring are hornless, and the grandchildren 3 hornless to 1 horned. The horned grandchildren breed true. No intermediates occur. Clearly one unit-character difference exists between horns and no horns. Therefore no stable intermediate class can exist unless this unit-character changes. This they consider to be impossible. If we call attention to a *short*-horned race as evidence

that the horn character may vary, they assure us that
this condition is due to a different unit and is not deriv-
able from the other, and they challenge us to produce it
from the other. If we begin measuring the horns of our
cattle and picking out those a little shorter than the
average, we find that offspring are obtained with horns
of practically average length. Perhaps we repeat the
selection half-a-dozen times and begin to get a barely
appreciable result. They interrupt, ''See here,'' they
say, ''you're not getting anywhere; give up and acknowl-
edge yourself beaten. If you stop your selecting for a
single generation, the little you have accomplished will
disappear. See meantime what we mutationists have ac-
complished; we have dehorned half-a-dozen breeds by
simple crossing. This is more than you could do in a
thousand years.'' Such comment on our work is ex-
tremely disquieting, for our progress *is* slow, and we can
only reply, ''Your method is the quicker one to get rid
of a character altogether, but you admit yourself power-
less to create a condition which you do not possess fully
realized at the outset. We do not admit ourselves so
helpless; we hope to get something which we do not now
have, and we are willing to wait a while for it. We be-
lieve that we can create what does not now exist. This
you confess yourself powerless to do.''

The foregoing states fairly, I think, the present views
regarding selection as a tool of the breeder held on one
hand by the mutationists and pure-line advocates, and
on the other hand by a minority of Mendelians who like
myself consider selection an important creative agency
in breeding.

The fundamental point of difference between these two
views lies in their different conception of unit-characters.
To the mutationist unit-characters are as changeless as
atoms and as uniform as the capacity of a quart meas-
ure. Theoretically an atom is an atom under all circum-
stances, and a quart holds the same anywhere and every-
where. But the worldly-wise know that the actual quart
is not the same in all places; it is apt to be smaller at the

corner grocery than in the U. S. Bureau of Standards, and the dishonest tradesman will select effectively for diminished size among the various quart measures offered on the market, unless his selection is carefully restrained by legislation. Similarly *actual* unit characters are modifiable under selection; only one blindly devoted to a contrary theory will be able long to shut his eyes to this fact. For several years I have been engaged in attempts to modify unit-characters of various sorts by selection and in every case I have met with success.

I shall speak first of the case least open to objection from the genotype point of view which requires:

1. That no cross breeding shall attend or shortly precede the selection experiment, lest modifying units may unconsciously have been introduced, and

2. That only a single unit-character shall be involved in the experiment.

These requirements are met by a variety of hooded rat which shows a particular black and white coat-pattern. This pattern has been found to behave as a simple Mendelian unit-character alternative to the self condition of all black or of wild gray rats, by the independent investigations of Doncaster and MacCurdy and myself. The pigmentation however in the most carefully selected race fluctuates in extent precisely as it does in Holstein or in Dutch Belted cattle. Selection has now been made by Dr. John C. Phillips and myself through 12 successive generations without a single out-cross. In one series selection has been made for an increase in the extent of the pigmented areas; in the other series the attempt has been made to decrease the pigmented areas. The result is that the average pigmentation in one series has steadily increased, in the other it has steadily decreased. The details of the experiment can not be here presented, but it may be pointed out (1) that with each selection the amount of regression has grown less, *i. e.*, the effects of selection have become more permanent; (2) that advance in the upper limit of variation has been attended by a like recession of the lower limit; the total range of varia-

tion has therefore not been materially affected, but a progressive change has been made in the mode about which variation takes place.

3. The plus and minus series have from time to time been crossed with the same wild race. Each behaves as a simple recessive unit giving a 3:1 ratio among the grandchildren. But the extracted plus and the extracted minus individuals are different; the former are the more extensively pigmented.

4. The series of animals studied is large enough to have significance. It includes more than 10,000 individuals.

The conclusion seems to me unavoidable that in this case selection has modified steadily and permanently a character unmistakably behaving as a simple Mendelian unit.

In my experience *every* unit-character is subject to quantitative variation, that is, its expression in the body varies, and it is clear that these variations have a germinal basis because they are inherited. By selection plus or minus through a series of generations we can intensify or diminish the expression of a character, that is, we can modify the character.

In an earlier lecture I showed that long hair and rough coat in guinea-pigs each differ from the normal condition by a single unit-character. In 1906 I showed that both these characters are subject to quantitative variation, and that such variations are heritable. The same is true of polydactylism in guinea-pigs, a condition in which a fourth toe is present on the hind-foot. A polydactylous race of guinea-pigs was unknown until I created one by selection from among the descendants of a single abnormal individual which had a rudimentary fourth-toe on one hind-foot. For several generations in succession those individuals were selected for parents which had the best-developed extra-toe, and thus was obtained a good 4-toed race.

Another character built up slowly from small beginnings is the silvered variety of guinea-pig. It originated

from a tricolor race in which was observed an individual having white hairs interspersed with red on the lower side of the body. Selection has been made to increase the amount of the silvering and to get it on a black background. This involved increase of the black areas in the coat as also of the silvered areas. In this task, difficult because it involved simultaneous modification of two unrelated characters, steady progress has been made. The best animals are now silvered all over except at the extremities.

Even albinism, the first-discovered of all Mendelian characters in animals and by every one acknowledged to be a single and simple unit-character, even this is variable. In rabbits, for example, some albinos are snow-white without a trace of pigment in the fur or skin, while others (the so-called Himalayan type) are heavily pigmented at the extremities (nose, ears, feet and tail). And yet we can not discover that these two kinds of albinism differ by any second unit-character which might account for the difference. Their albinism is different. Between the extreme types of the snow-white and the Himalayan albino, various intermediates exist, but all are clearly albinos, producing only albinos when bred *inter se*. They represent quantitative variation within the albino type.

Similar quantitative variation within colored classes of animals is well known. Thus in mice an extreme quantitative reduction of the pigmentation has produced an animal with pink eyes and faintly colored coat. Such an animal, however, is not an albino, though less heavily pigmented than many Himalayan rabbits, for if the pink-eyed mouse is crossed with an albino, fully pigmented young result.

In guinea-pigs I several years ago set myself the task of reducing as much as possible the pigmentation of a black race, in hopes thus of obtaining blues. I first crossed the blacks with a light yellow (cream-colored race). In the heterozygotes the black was somewhat reduced in amount. The lightest of these were selected

and again crossed with yellow. By this means the black was after several generations much reduced. The hairs were distinctly yellowish at base and the part above sooty black in appearance. Recently a pink-eyed animal has appeared in this race with hair light sooty-black in spots. This evidently is an extreme variation in the direction which selection has taken throughout the experiment and probably similar in nature to the pink-eyed variation in mice. There can be no question of recombination of independent Mendelian factors in this experiment, because (aside from albinism) only a single Mendelian factor is involved. The heterozygotes, as regards black, have consistently behaved as *simple* heterozygotes, and the experience of all observers agrees with my own that black in guinea-pigs is a simple Mendelian unit. If so it is clearly a unit modifiable under selection.

In yellow animals, as in blacks, individuals of varying intensity occur, the darkest known as reds, the lightest as creams. A complete series of intermediates can be obtained if so desired. If we select any two widely separated stages in this series fairly stable in their breeding capacity and cross these, they Mendelize, *i. e.* they behave as if there were a single unit-character difference between them. Now this fact is instructive, for it throws light on the nature of unit-characters in such cases. They are not things in themselves distinct and separate from the organism concerned; each is a *quantitative variation* plus or minus in some one character possessed by the organism. Each quantitative condition of a character tends to persist from cell-generation to cell-generation. When two quantitatively unlike conditions of a character are brought together in a fertilized egg, they tend to keep their distinctness in subsequent cell-generations and to segregate into different gametes at reproduction, *i. e.,* they Mendelize. Only by a figure of speech are we justified in recognizing a *unit* difference between them. That difference might equally well be *half* as great as it is, or a *quarter* as great, or a thousandth part as great. A mono-hybrid ratio would result

equally in each case, upon crossing the two quantitatively different stages. It is the substantial integrity of a quantitative variation from cell-generation to cell-generation that constitutes the basis of Mendelism. All else is imaginary.

We can distinguish and trace the history of these quantitative variations from generation to generation only when the differences between them are of some size. This has led many to think that only variations of some size are inherited (the mutation theory) and others to deny that such variations can be increased in size by selection (the genotype theory). Others still observing unmistakable evidence that small variations are heritable no less than large ones conceive that the large variations which can be increased or decreased by selection are composed of a certain number of smaller ones cumulative in their effects (the multiple factor hypothesis). A fatal objection to this idea is the fact that these quantitative variations behave as *simple* units, not as multiple ones, and so give mono-hybrid ratios, not polyhybrid ones. The only logical escape from this dilemma for one devoted beyond recall to a pure-line hypothesis will be to assume further that the assumed multiple units are all coupled, *i. e.*, all united in a single material body so that in cell-division they *behave* as one unit, for practical purposes are one unit. This position will be *logically* unassailable, for we shall never know whether the body which in practise behaves as one is in the last analysis composite. Chemists tell us (or used to) that water is composed *ultimately* of atoms of hydrogen and atoms of oxygen not further dissociable, uniform in size and weight and hard and indestructible as rocks; nevertheless for practical purposes we *drink* our cup of water and do not *chew* it. I for one will be content with the admission that variation is as continuous as water and will not press the argument against discontinuity into realms of the ultimate.

The majority of the characters dealt with by the animal breeder are less simple in behavior than color char-

acters. They are also from the economic standpoint more important. Their careful study is therefore desirable. Several years ago I undertook the study of size inheritance in rabbits. I found that when rabbits of unequal size are mated, the young are of intermediate size, *i. e.,* neither large nor small size dominates in the cross. Further, segregation does not apparently occur among the grandchildren, for these vary about the same intermediate mode as the children, though somewhat more extensively. My conclusion was that the inheritance in such cases is non-Mendelian, since neither dominance nor segregation occurs. I called it blending. The experiment with rabbits has been repeated on a much larger scale by my pupil, Mr. E. C. MacDowell. He finds, however, that the variability of the grandchildren is considerably greater than that of the children, though it seldom extends far enough to include the extreme conditions found in the grandparents. This result is confirmed by observations upon ducks made by Dr. Phillips. It is evident therefore that size is not a simple unit-character, for there is no dominance and no evidence of segregation other than the increased variability of the second hybrid generation. But cases of this kind have recently been interpreted as involving multiple unit characters and so as possible Mendelian. This interpretation has been suggested by interesting observations made by Nilsson-Ehle on color-inheritance in oats and wheat.

In crossing colored with uncolored varieties he obtained inheritance ratios of 15:1 or 63:1, instead of the usual 3:1 of colored to uncolored progeny in the second generation from the cross. The ratios obtained in these exceptional cases were such as should occur when two or three independent unit-characters are involved in a cross. But Nilsson-Ehle could discover only a single kind of color-production. The conclusion which one naturally draws from these facts is that the color factor in these cases was localized in two or three distinct bodies independent of each other in their splittings and migrations during cell division. Now Nilsson-Ehle argues with much plaus-

ibility that if in a case such as this dominance were
wanting, *i. e.*, if the cross always produced intermediates,
the bulk of the second-generation offspring would also be
intermediate, with only an occasional complete segrega-
tion. He suggests that size differences may involve units
of this sort, without dominance though fully segregating.
This attractive hypothesis would account for the known
facts of size inheritance fairly well, involving only the
existence of multiple units which may be perfectly stable
and changeless in character. Nevertheless this hypothe-
sis has not been established beyond question. It is quite
possible that we are stretching Mendelism too far in
making it cover such cases. Dominance is clearly absent
and the only fact suggesting segregation is the increased
variability of the second as compared with the first hy-
brid generation. This fact however may be accounted
for on other grounds than the existence of multiple units
of unvarying power.

If size differences are due to quantitative variations
in special materials within the cell, it is not necessary to
suppose that these materials are localized in chunks of
uniform and unvarying size, or that they occur in any
particular number of chunks, yet the genotype hypothe-
sis involves one or both of these assumptions. Both are
unnecessary. Variability would result whether the
growth-inducing substances were localized or not, pro-
vided only they were not homogeneous in distribution
throughout the cell. Crossing would increase variability
beyond the first generation of offspring because it would
increase the heterogeneity of the zygote in special sub-
stances (though not its total content of such substances)
and this heterogeneity of structure would lead to greater
quantitative variation in such materials among the
gametes arising from the heterozygote. Thus greater
variability would appear in the second hybrid genera-
tion.

As a matter of fact we know that protoplasm is not
homogeneous, and that there are substances widely distri-

buted in the cell, not localized in chromosomes, which may well have an influence on size.

But whatever our conclusion may be concerning the theoretical explanation of size inheritance, the practical manipulation of it must clearly be different from that of color inheritance. All possible combinations of color factors existing in two distinct races we can secure within two generations by crossing. New conditions of color we can often obtain by the slower process of selection, thus modifying existing color factors. Modification is, I believe, often accelerated by crossing, quite apart from the effect it has in bringing about recombination, because it has a tendency to increase quantitative variation.

Size is an unstable character, ever varying. Slow changes in size can be effected by selection without any crossing whatever. Change in size is made more rapid by crossing, because variability is increased thereby. If further increase in size is desired regardless of other qualities two large races should be crossed and the largest second-generation offspring should be selected. Progressive diminution in size should be sought in a similar way, crossing the smallest breeds.

If a medium-sized race is desired, it may be obtained by crossing a large with a small race and inbreeding the offspring. Physiological limitations undoubtedly would prevent unlimited size variations either plus or minus, yet when we consider what extreme differences exist among dogs, as for example between "toy terriers" and "great Danes," we can scarcely doubt that the limits of possible size variation have not been approached in most of our domesticated animals.

SHORTER ARTICLES AND DISCUSSION

INHERITANCE OF COLOR IN THE ALEURONE CELLS OF MAIZE

In those plants of which there is a considerable knowledge of the heredity of flower sap color, namely, *Antirrhinum, Lathyrus, Matthiola* and *Primula,* it has been found that an hypostatic color factor is often necessary for the production of an epistatic color. For example, a basic factor generally designated as *C* being present, a flower becomes red by the addition of a factor *R,* and becomes magenta or purple by the addition of still another factor *P.* The zygotic formula of a pure red flower is *RRCC* and of a pure purple flower is *PPRRCC;* but a flower with the zygotic formula *PPCC* is colorless.

On the other hand, certain seed coat and other colors of wheat, of beans and of other plants do not need the presence of the hypostatic factor for the formation of the epistatic color. For example, Nillson-Ehle crossed a black glumed oat *BBGG* with a white glumed oat *bbgg.* In the F_2 he obtained 12 black : 3 gray : 1 white. The actual ratio was $9BG : 3Bg : 3bG : 1bg$, but as the black was produced whether the gray factor was present or not, the visible ratio was as given above.

The natural conclusion is that in the first category the epistatic factor is more specific in its action than it is in the second category. If one accepts the interpretation that color is formed by the action of an enzyme on a colorless chromogen, he must conclude that the epistatic enzyme of the first kind can only produce its action, if, by the presence of the hypostatic enzyme, the chromogen has already been carried through a necessary preliminary reaction. An epistatic enzyme of the second kind, however, is sufficient unto itself and is absolutely independent of the action of the hypostatic enzyme. One may even assume that the chemical bases upon which the two enzymes of the second category act are independent of one another.

Perhaps a concrete illustration will show the difference of action in these two cases better than description. In the black glumed oat *BBGG,* one can imagine the black color or the gray color wiped out mechanically. The other color remains. In the

purple flower *PPRRCC*, if the red factor is wiped out no color is left.

In an earlier paper East and Hayes[1] found four independent gametic factors in maize, each of which affects the production of color in the aleurone cells of maize. These four factors are a basic color factor *C*, a reddening factor *R*, a purpling factor *P*, and an inhibiting factor *I* which prevents the development either of the red or of the purple color. Of the various points of interest in the interpetation of the inheritance of these factors, two have been investigated further. The first is the cause of modified colors. This will be discussed at length in another paper. The second is the action of the reddening factor *R* and the purpling factor *P*. It was then thought that the presence of the factor *P* together with *C* was all that was necessary for the production of the purple color. It can now be shown that the purple color develops only when the three factors *P*, *R* and *C* are present. The production of color in the aleurone cells of maize is therefore analogous to that in the flowers of the genera described above, which was designated as category one. This interpretation of the facts makes little difference in the general behavior of these colors in inheritance and is only interesting in so far as it unifies the interpretation of the aleurone colors in maize with the sap colors of certain flowers.

The following scheme will show the differences in behavior in the two schemes.

1. A purple crossed with a non-purple gives 3 purple : 1 non-purple in F_2. Here there is no difference in the two schemes. The proper interpretation gives this result from crosses

$$PPRRCC \times PPRRcc \text{ or}$$
$$PPRRCC \times PPrrCC.$$

2. A purple crossed with a non-purple gives 9 purple : 7 non-purple in F_2. The old interpretation was that this occurs when the F_1 has the formula *PpCc*. The present interpretation is that it occurs when the formula of the F_1 is *PPRrCc*.

3. A purple crossed with a non-purple gives the formula *PpRrCc* in F_1. If the *R* factor is unnecessary for the production of purple, the ratio in F_2 will be (*a*) 36 purple : 9 red : 19 white. If *R* is necessary for the production of purple the ratio in F_2 will be (*b*) 27 purple : 9 red : 28 white. A sample

[1] "Inheritance in Maize," *Conn. Agr. Exp. Sta. Bull.*, 167: 1–141, 1911

family of F_2 segregates gave the following ratio which may be compared with the closest possible expectancy under each theory.

Actual result .... 191 purple : 56 red : 180 white.
Theory (*a*) .... 240 purple : 60 red : 127 white.
Theory (*b*) .... 180 purple : 60 red : 187 white.

This suggests theory *B*, but is not conclusive. Conclusive evidence comes from the F_3 generation. On theory *A*, every 36 purple F_2 seeds should give on the average the following results in F_3:

4 ears all purple.
10 ears segregating 3 purple : 1 white.
4 ears segregating 9 purple : 7 white.
2 ears segregating 3 purple : 1 red.
4 ears segregating 12 purple : 3 red : 1 white.
4 ears segregating 9 purple : 3 red : 4 white.
8 ears segregating 36 purple : 9 red : 19 white.

On theory *B*, every 27 purple F_2 seeds should give on the average these results in F_3:

1 ear all purple.
4 ears segregating 3 purple : 1 white.
2 ears segregating 3 purple : 1 red.
4 ears segregating 9 purple : 7 white.
8 ears segregating 9 purple : 3 red : 4 white.
8 ears segregating 27 purple : 9 red : 28 white.

The crucial test is the appearance of families showing the ratio 12 purple : 3 red : 1 white. No such family has ever appeared. On the other hand they did divide nicely into families with ratios of 9 : 3 : 4 and 27 : 9 : 28. Of the first type the total progeny of nine families was 935 purple : 318 red : 436 white. The closest theoretical ratio on the basis of 9 : 3 : 4 would be 950 purple : 317 red : 422 white. Of the second type the total progeny of four families was 423 purple : 127 red : 396 white. The closest possible ratio on the basis of 27 : 9 : 28 would be 400 purple : 133 red : 414 white.

All other tests made corroborated the interpretation that the *P* factor can produce purple only when *R* and *C* are present.

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NUCLEAR GROWTH DURING EARLY DEVELOPMENT

In reading Conklin's recent paper on the relative growth of nucleus and cytoplasm in developing eggs,[1] I was at first somewhat puzzled by certain of the relations brought out. The matter is one that bears directly upon so many important problems, and Conklin's paper is one of such fundamental importance, that possibly a statement of the difficulty and its apparent solution may be worth while. Work done with the thoroughness that characterizes all that Conklin puts forth partakes to a certain degree of the inexhaustibleness of nature, in that it is possible to discover in it relations not explicitly set forth by the author.

Conklin's most notable result is that the relative proportions of nuclear and cytoplasmic materials do not appreciably change during early development, as they have been supposed to do. The bearing of this upon the theory that cleavage is a process of rejuvenescence, owing to the enormous increase of nuclear material relative to the cytoplasm, is evident. The point which I wish to discuss has no bearing upon this fundamental result, but relates to the rate of nuclear growth.

On this point Conklin sums up his results for *Crepidula* as follows:

"The rate and amount of nuclear growth during cleavage is much less than is generally believed. Whether the nuclear volume is taken when the nuclei are at their maximum, mean or minimum size, the nuclear growth is far from 100 per cent. or a doubling, in each division. In *Crepidula* the nuclear growth is not more than 5 per cent. to 9 per cent. for each division from the 2-cell to the 32-cell stage, and less than 1 per cent. for each division after the 32-cell stage" (p. 40).

Similar figures are given for the other animals studied.

Now, if I have gotten clear on the matter, what Conklin here means is that when any cell divides, the increase of nuclear material thus produced is on the average but 5 to 9 per cent. *of the amount that was present in an early stage of the egg, and specifically in the two-cell stage.* This is a different method of expressing the rate of growth from that often employed. The question perhaps most often answered when the rate of nuclear growth at cell division is given is the following: How much is

[1] Conklin, E. G., "Cell Size and Nuclear Size," *Journal of Experimental Zoology*, *12*, 1–98.

the nuclear material of a given cell increased when that cell divides? Or, what is essentially the same, when several cells are present, as usually in a developing egg: In what proportion is the total nuclear material increased when all of the cells divide once? It appears to me that these questions are the ones that have been in mind when it has been held that the nuclear material increases nearly 100 per cent. at each cleavage, so that the relation of the ratio used by Conklin to the ratio implied by them is of interest.

The ratio implied in the questions just set forth—the ratio of increase in the nuclear material of a given cell after that cell has divided—is of course obtained by dividing the nuclear volume of the two resulting cells by this volume in the mother cell; or by dividing the total nuclear volume of the egg after all its cells have divided once by the total volume before the cells divided. (Inclusion of several cells, each of which divides once, of course does not of itself alter the ratio.) Performing these operations for the mean nuclear volumes in *Crepidula,* as given in Conklin's Table 9, one finds the ratios in question to be for the second cleavage 1.40, for the third 1.25, for the fourth 1.19, for the fifth 1.89. That is, in passing from the 2-cell to the 4-cell stage, the nuclear volume of each mother cell increases 40 per cent.; in passing from the 4-cell to the 8-cell stage, the increase is 25 per cent.; from the 8- to the 16-cell stage it is 19 per cent.; from the 16- to the 32-cell stage it is 89 per cent. These ratios are not 100 per cent. at each division, but they approach it more nearly than the ratio Conklin employs. If we average the increase for these four cleavages, we find the mean to be 43 per cent. That is, at each cleavage, the nuclear volume of the cell increases on the average by 43 per cent.

It may be noted that even with an absolutely constant ratio between the nuclear volume in a given cell before cleavage and that in its products after cleavage, the ratio employed by Conklin would, as a rule, if I have correctly interpreted it, decrease rapidly as we pass to later cleavage stages. The relation between the two ratios would be that shown by the following formula, in which $x =$ Conklin's ratio; $r =$ the (constant) ratio of the nuclear volume after division of a given cell to the nuclear volume before that division; $n =$ the number of the cleavage (1, 2, 3, etc.) :

$$x = \frac{r^{n-1} - 1}{2^n - 2} \cdot \tag{1}$$

For example, if $r = 1.5$ (so that the nuclear volume of any cell increases 50 per cent. when that cell divides), then for the result of four cleavages (producing 16 cells) the formula gives

$$x = \frac{(1.5)^3 - 1}{2^4 - 2} = \frac{2.375}{14} = 16.96 \text{ per cent.}$$

If Conklin employed the 1-cell stage as his standard of comparison, the above formula would be

$$x = \frac{r^n - 1}{2^n - 1}. \qquad (2)$$

It will be found that for any increase less than 100 per cent. of what was present before division (that is, $r = 2$), Conklin's ratio (from formula 1 or 2) decreases in the later stages of cleavage, even though the law of increase, so far as each cell by itself is concerned, remains absolutely the same. Thus, if at the division of every cell its nuclear volume increases 50 per cent., Conklin's ratio (formula 1) will give 25 per cent. for the result of the second cleavage, 20.83 for the third, 16.96 for the fourth, 13.54 for the fifth, 10.64 for the sixth, 8.25 per cent. for the seventh, etc. This appears to be the reason why Conklin finds the rate of nuclear increase, as shown by his ratio, to be less in later stages; it is not due to any change in the relations so far as what happens in each cell is concerned.

<div align="right">H. S. Jennings</div>

IS THERE ASSOCIATION BETWEEN THE YELLOW AND AGOUTI FACTORS IN MICE?

In the generally accepted formulæ for the colors of mice, as worked out by Cuénot, Bateson, Durham and others, there is assumed to be a factor, Y, for self yellow color,[1] which is epistatic to T, the ticking or agouti factor (also known as G). The various types have the following constitution:

Yellow .... $Yt\ yt$, or $Yt\ yT$.[2]
Agouti (including cinnamon) .... $yT\ yT$, or $yT\ yt$.
Black and chocolate (including dilute forms) .. $yt\ yt$.[3]

[1] On the formulæ adopted here this factor Y is probably to be considered an inhibitor.

[2] It has been shown by Cuénot and others (see especially Castle and Little, *Science*, N. S., 32, 868, 1910) that mice homozygous for Y do not exist, the reason probably being that the YY zygotes, though formed in the expected proportions, do not develop.

[3] Blacks differ from chocolates in having a black factor, B. Agoutis also carry this factor, while cinnamons lack it. Yellows may or may not bear it, but the two types are distinguishable by their eye color.

If yellow mice of the sort one usually obtains be bred together they produce yellows, blacks and chocolates—almost never any agoutis. But if such yellows be bred to agoutis and their yellow offspring be mated together the result is only yellows and agoutis. It has been pointed out by Morgan[4] that this last result is inconsistent on the current formulæ, since blacks or chocolates should also be expected. For example, if we assume, as I think we must, that ordinary yellow mice usually have the constitution *Yt yt*, then the cross under discussion would be as follows:

$$\text{Yellow}—Yt\ yt$$
$$\text{Agouti}—yT\ yT$$

$$Yt\ yT—\text{yellow}$$
$$yt\ yT—\text{agouti}$$

F$_1$ yellow—gametes—*YT Yt yT yt*

YT YT	YT Yt	YT yT	YT yt
Yt YT	Yt Yt	Yt yT	Yt yt
yT YT	yT Yt	yT yT	yT yt
yt YT	yt Yt	yt yT	yt yt

F$_2$

Total, omitting all *YY*'s: 8 yellows, 3 agoutis, 1 black or chocolate.

It seems to me that the easiest way of explaining why this mating actually does not produce blacks and chocolates is by the assumption of linkage or association (''gametic coupling'') between the agouti and yellow factors. The fanciers, from whom most yellows come, ordinarily keep few agouti mice. It is therefore probable that most yellows carry no *T*, and for this reason *Y* and *T* really show ''spurious allelomorphism'' or repulsion instead of ''gametic coupling.''[5] There seems to be no evidence that *Y* and *T* ever occur in the same gamete. The evidence which has led to this conclusion is as follows:

Miss Durham[6] has found that if ordinary yellows be mated

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[4] *Ann. N. Y. Acad. Sci.*, 21, 87, 1911. It was at Professor Morgan's suggestion that I took up this problem.

[5] I shall use the term association to cover both coupling and repulsion.

[6] *Journ. Genet.*, 1, 159, 1911.

together they produce two yellows to one black or chocolate, no *T* being present. Her total figures are 451 yellows to 241 blacks and chocolates, to which should be added Little's[7] record of 31 yellows to 24 blacks and chocolates. If ordinary yellows be mated to chocolates or blacks the result is an equal number of yellows and of blacks or chocolates. Miss Durham's figures are 282 yellows and 319 blacks and chocolates. Both these crosses are cases of monohybridism, *T* never being present, and *Y* alone being involved.

If ordinary yellows be bred to pure agoutis, the result should be equal numbers of yellows and agoutis, as shown above. The actual results obtained are as follows:

Yellow	Agouti	Authority
53	39	Durham.
16	14	Morgan.
69	53	

If the P_1 agouti used in this cross were heterozygous in *T*, then the expectation would be two yellows, one agouti, and one black (or chocolate). Apparently Morgan is the only one who has reported such a cross. He obtained 4 yellows, 5 agoutis, and 1 black.

The results of the four crosses above are explicable without the assumption of association between *T* and *Y*, since in no case was an animal bred from which was heterozygous in both, and only in such cases does association ever become apparent. But such heterozygous mice should be obtained in the cross between agouti and yellow. If these be mated together the ordinary expectation, as shown by the diagram above, would be 8 yellows, 3 agoutis, and 1 black or chocolate. The actual offspring recorded from yellow by yellow giving agouti are:

Yellow	Agouti	Black and Chocolate	Authority
108	62	0	Durham.
15	9	0	Morgan.
123	71	0	

This is approximately two yellows to one agouti. It is the result which would be expected if one of the parent yellows were pure for *T* (*TY Ty*). But, with the possible exception of 20 of Miss Durham's,[8] all the above 194 mice were from yellows out of yel-

[7] *Science*, N. S., 33, 896, 1911.

[8] It would appear from the context that these 20 also belong to the category under discussion, but a definite statement to that effect is not given.

low by agouti. No other crosses of yellow by yellow gave agouti, so that it seems in the highest degree probable that the original (P_1) yellows were pure for t. That being the case the F_1 yellows must all have had the formula $tY\ Ty$. But since they produced only $\frac{2}{3}$ yellows to $\frac{1}{3}$ agoutis it follows that association occurs between T and Y, thus:

$$
\begin{array}{l}
\text{Yellow}\!-\!tY\ Ty \\
\text{Yellow}\!-\!tY\ Ty \\
\hline
\quad\quad Ty\ tY \\
\quad\quad tY\ Ty \!-\!2\ \text{yellows.} \\
\quad\quad (tY\ tY) \\
\quad\quad Ty\ Ty\!-\!1\ \text{agouti.}
\end{array}
$$

These T-bearing yellows have also been bred to chocolates and blacks. If there were no association this mating should produce two yellows, one agouti, and one chocolate or black. But Miss Durham has obtained only 30 yellows and 37 agoutis—practically equal numbers, with no blacks or chocolates. On the association hypothesis this cross should produce the following result:

$$
\begin{array}{r}
\text{Yellow}\!-\!tY\ Ty \\
\text{Chocolate or black}\!-\!ty\ ty \\
\hline
tY\ ty\!-\!1\ \text{yellow.} \\
Ty\ ty\!-\!1\ \text{agouti.}
\end{array}
$$

Apparently the ticking factor and the factor which produces yellow mice are associated very closely. There appears to be no evidence that "crossing over" ever occurs. It can not be supposed that Y is the same as t, with which it always occurs, since in that case all mice not agouti, or even heterozygous for T, would be yellow, and black and chocolate would not exist. It should be noted that if one adopts Castle's mouse formulæ (see Castle and Little,[9] etc.), it is still necessary to suppose that association occurs but now between the restriction factor, R, and the agouti factor, A.

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COLUMBIA UNIVERSITY,
    February, 1912

[9] *Science*, N. S., 30, 313, 1909.

THE MALTHUSIAN PRINCIPLE AND NATURAL SELECTION

In the last edition of his essay on population, page 2, Malthus laid down the following biological proposition from which he derived his well-known sociological conclusion:

The cause to which I allude is the constant tendency in all animated life to increase beyond the nourishment prepared for it.

It is incontrovertibly true that *there is no bound to the prolific plants and animals, but what is made by their crowding* and interfering with each others' means of subsistence.   (Italics mine.)

In plants and irrational animals, the view of the subject is simple. They are all impelled by a powerful instinct to the increase of their species; and this instinct is interrupted by no doubts about providing for their offspring. Wherever, therefore, there is liberty, the power of increase is exerted; and the superabundant effects are repressed afterwards by want of room and nourishment.

The great influence of this book upon Darwin is well known and so it is not surprising to find him writing in the "Origin of Species," page 60,

A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase.

And again on page 72,

Each organic being is striving to increase in geometrical ratio; each, at some period of its life, during some season of the year, during each generation or at intervals, has to struggle for life and to suffer great destruction.

It is quite natural, therefore, to find that in the current texts and in the class room, that natural selection is taught as starting from the contrast of a limited subsistence and a very large birth-rate (and I confess that I have been guilty). So strong an impression is thus made, that to most people, and unfortunately many sociologists, natural selection has come to mean that factor of evolution which is caused by an excessive birth rate.

The fact is frequently lost sight of that natural selection effects its results by differential success in mating (sexual selection), and differential fecundity (fecundal selection), as well as by a differential age at death (lethal selection). Even when we confine our attention to lethal selection, we shall see that a very large share of its action is in no way dependent upon the adequacy of the food supply. Such selection may well be called non-

sustentative selection to distinguish it from that which is so dependent.

Sustentative selection is generally thought to be nearly always in operation. In every group of animals in which I have made any special field observations, namely, bryozoa, birds and beetles, the falsity of this belief has been impressed upon me. With fresh-water bryozoa the food supply can scarcely ever be taxed. The limiting conditions seem to be largely inconstancy of the bodies of water, the danger of being eaten, and the limited extent of suitable substrata.

With birds, when one really sees an emaciated individual, the result of some accident which has made it difficult for it to obtain food, one is struck by the very great contrast with other birds. In my experience, in skinning birds in the state of Washington, summer and winter, I never opened one not well equipped with abdominal fat. On the other hand, the great loss of the young birds by adverse weather and the large variety of predaceous enemies is common knowledge.

With lady beetles there is a more direct relation of the numbers to food supply, but even here it is a question of finding food, rather than any real lack of it. The food supply of the adult beetles, embracing aphids, pollen and spores, is superabundant. The principal causes of death seem to me to be due to inability of the females to distribute the eggs proportionately to the distribution of aphids, and, secondly, the unreliableness of aphid stocks, owing to their rapid annihilation when one of the numerous aphid diseases or parasites becomes rampant. One may often hunt over many colonies of aphids without finding any coccinellid larvæ, and then at last find one of the same species with several large egg masses. So many larvæ will hatch in this case that they will consume all the aphids before they themselves have all become mature. As a result, they will wander, only a few surviving who may have the efficient instincts and good fortune necessary to discover another stock of aphids.

Of the half dozen or so species of the large coccinellids most common in the United States, it is common to find here one species abundant, and there another, though some others are also found. Attempts to account for these contrasts in numbers on grounds of temperature, humidity, altitude and the like, have proved unsuccessful. I think it is because the instincts of egg-laying and of migration of the larvæ of one species or another is better adapted to the species of aphids and aphid-affected plants

in that vicinity. Evidence to this effect is seen in the fact that
certain shrubs that are aphis-infected for a short time only in the
early spring sustain only *Adalia bipunctata*. The wild parsnip,
which becomes infected with other aphids later, sustains *Adalia
bipunctata* in numbers smaller than three of its competitors. If
we take the herbivorous coccinellids, we will find similarly in
some places an abundance of food that they have not touched,
while some other patches of suitable plants may be stripped.

In conclusion, then, we see that in the bryozoa and birds,
sustentative selection does not play the dominant rôle imputed to
it. In the lady beetles, where the supply of food is seen to limit
their numbers, it is not because there is not food enough, but
because the individuals are not properly distributed with refer-
ence to that food. The sustentative selection in this case must be
differentiated as indirect. The evolutionary significance lies in
the fact that where the sustentative selection is indirect, the
species may become more abundant through variations which ad-
just the individuals better to the food supply.

I believe there is a fundamental reason for this subordination
of sustentative selection. The reproductive rate is not merely
an arbitrarily large number, which necessarily causes a severe
struggle, but is just such a number as is best adapted, in general,
to the needs of the species. The extreme members of that school
which emphasizes the importance of the variations at the expense
of selection can scarcely object to this, for fecundity is always
variable and these differences are known to be inheritable in
many cases.

Now the number of progeny which is best adapted to the needs
of the species is that number which is large enough to sustain
the losses from all non-sustentative causes of death, but not large
enough to invoke death by starvation. Such a species is obvi-
ously less liable to extermination than one in which the hostile
influence of underfeeding always handicaps. If grasshoppers
conformed to the Malthusian conceptions of many evolutionists,
there should be no alfalfa, for that favorite food would all be
eaten up before it could be harvested. The world teems with
herbivorous animals of one kind or another, and yet also teems
with plants, most of which are eaten by many species of animals.
I can see no other explanation than that the species are not ordi-
narily subject to sustentative selection, and that when it is, it is
generally the indirect selection rather than the direct.

Indirect sustentative selection is less injurious to a species, be-

cause those individuals which do become well placed thrive. The burden of starvation passes by a number of the individuals to fall upon the others. In this way, the evil effects of a general underfeeding, which is the necessary result of direct sustentative selection, is avoided. In cases, then, where indirect sustentative selection is operative, the reproductive rate is that which will produce enough individuals to find many of the favored places and withstand the non-sustentative causes of death. Where direct sustentative selection might be theoretically expected, as in the case of the large birds of prey, in regions where they are not persecuted, the rigors of a possible struggle are avoided by low reproductive rates.

While the reproductive rate must be looked upon as a characteristic which has its adaptations like other characteristics, it has one peculiarity—its increase is always opposed by lethal selection. The chances of life are reduced by reproducing inasmuch as more danger is entailed by the extra activities of courtship, and later, of the care of the young, since they reduce the normal wariness of individual life. The species, therefore, always keeps the reproductive rate at the lowest point which will suffice for the reproductive needs of the species. For this reason alone we should expect the non-sustentative selection to be the predominant kind.

Gulick and Pearson have shown that there is a normal conflict between natural selection and fecundal selection. Fecundal selection is said by them to be constantly tending to increase the reproductive ratio, while lethal selection asserts its power to reduce it, because the reproductive demands on the parents reduce their chances of life by interference with their natural ability of self-protection. This is quite true, but the analysis is incomplete, for an increased number of progeny not only decreases the life chances of the parents, but also of the young, by reducing their endowment and care.

A further reason for believing in the predominance of non-sustentative selection is the fact that the species that have evolved furthest are well known to be of low fecundity. Man, himself, even where there is no artificial restraint, has one of the smallest reproductive rates known. If sustentative selection had been predominant, we should expect higher fecundities in these highly evolved species than in the lower ones.

The fundamental formula of Malthusianism, that the number of individuals in a species tends to increase in geometrical ratio,

is misleading, and a great mass of biological and sociological writing has been led into error by it. Of course, there can be no objection to the position that since the number of progeny exceeds the number of parents, there must be many premature deaths, or the species will increase in numbers. But this is a truism. The real essence of Malthusianism lies in the conclusion that a sustentative struggle must arise, and there lies the error. The Malthusian conception of the rate of reproduction is that the rate is such that the food supply must be overtaxed and a struggle for existence will take place. The conception here urged is that each species has such a reproduction rate as will suffice to withstand the premature deaths and sterility of some individuals, and yet not so large as to press normally upon the limits of the food supply.

I believe the common over-estimation of the rôle of sustentative selection, and the neglect of the non-sustentative, is largely historical in origin, and that it is maintained by improper teaching.

In teaching natural selection, the fault is generally made of starting with the Malthusian contrast between the limitation of the food supply and the rate of reproduction. The current conception will not be righted until we learn to teach natural selection more correctly. While the rate of reproduction is the proper place from which to start, this should be treated, not as a fixed quantity to which nature must accommodate itself, but as that number which just exceeds the great number of premature deaths and suffices to replace the parents. Then the premature death of the 999 must be explained. After an examination of these causes the student can not but grasp the master rôle of the non-sustentative form.

Finally, then, we see from these considerations, that the common assumption that every species is as common as it can be, because it is living up to the limits of subsistence is erroneous. A relaxation of any of the causes of death in most cases will increase the numbers.

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